The generic delimitation of *Lachnaea* and *Cryptadenia* (Thymelaeaceae)

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ABSTRACT

The current generic delimitation of *Lachnaea* L. and *Cryptadenia* Meisn. was investigated. A multidisciplinary approach was followed. This included a study of the habit, phyllotaxis, morphology and anatomy of the leaves and flowers, pollen morphology and karyology.

No major differences were found between the two genera. The range of variation of certain diagnostic characters of these genera is such that the genera merge into each other. It was concluded that the two genera are congeneric and the inclusion of *Cryptadenia* within *Lachnaea* is proposed.

UITTREKSEL

Die huidige generiese afbakening van *Lachnaea* L. en *Cryptadenia* Meisn. is ondersoek. 'n Multidissiplinêre benadering is gevolg. Die groeiwyse, blaarstand, morfologie en anatomie van die loofblare en blomme, stuifmeelmorfologie en kariologie is bestudeer.

Geen noemenswaardige verskille tussen die twee genera is gevind nie. Die variasiegradiënt van sekere diagnostiese kenmerke van hierdie genera is van so 'n aard dat die twee genera oorvleuel. Die insluiting van *Cryptadenia* binne die omskrywing van die generiese grense van *Lachnaea* word voorgestel.

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INTRODUCTION

The genera *Lachnaea* L. and *Cryptadenia* Meisn. belong to the family Thymelaeaceae. Their close affinity is reflected by their placement in the different classification systems of the Thymelaeaceae (Endlicher 1847, sec. Domke 1934; Meisner 1857; Bentham & Hooker 1880; Gilg 1894 and Domke 1934). Only Baillon (1880) did not recognize *Cryptadenia* as a separate genus but treated it as a section of *Lachnaea*. He found that the flowers of *Lachnaea* varied from regular to irregular and that intermediate forms made it impossible to split the genus.

The genus *Lachnaea*, based on two species, was established by Linnaeus in 1753. In subsequent publications, such as Lamarck (1792, 1804), Salisbury (1808) and Sims (1813, 1814), new species were described, but only in 1840 was a detailed taxonomic account of the genus published by Meisner based on Drège's collections. Three sections were established, namely *Sphaeroclinium* Meisn., *Conoclinium* Meisn. and *Microclinium* Meisn., based on the inflorescence structure. Thirteen species and six infraspecific taxa were recognized (Meisner 1840). Meisner's earlier contribution on *Lachnaea*, with some alterations, was published in De Candolle's *Prodromus* in

which 18 species and 17 infraspecific taxa were recognized (Meisner 1857). The most recent taxonomic treatment of the genus was that of Wright (1915) in *Flora capensis*. In this treatment no mention was made of the sections established by Meisner. Wright (1915) recognized 19 species and eight infraspecific taxa, and referred to one imperfectly known species. In the Addenda to the same volume, a further two species and two infraspecific taxa were added (Wright 1925). Since then four new species have been described, namely three by Compton (1934a & b, 1953) and one by Fourcade (1934). When Thoday (1924) published the revision of the genus *Passerina*, he noted that the type of *Passerina laniflora* C.H. Wright was not a *Passerina* species but indeed a species of *Lachnaea*. Bond (1982) proposed the new combination, *Lachnaea laniflora* (C.H. Wright) Bond. *L. marlothii* Schltr. (Schlechter 1896) and *L. gracilis* Meisn. (Meisner 1840) were both overlooked by Wright. At present 29 species and eight infraspecific taxa are recognized (Van Wyk 1993).

The genus *Cryptadenia*, comprising five species, was established by Meisner in 1840 and was also based on Drège's collections (Meisner 1840). According to Meisner (1840) the main characters by which *Cryptadenia* can be distinguished from the closely related genus *Lachnaea*, are the glands which are positioned much lower down in the hypanthium just above the ovary, and by the conspicuous filaments which are adnate to the hypanthium. In De Candolle's *Prodromus* the same five species were recognized by Meisner (1857). The most recent taxonomic treatment of *Cryptadenia* was that of Wright (1915) in *Flora capensis*, in which four of the species in Meisner's treatment were recognised, whereas one was reduced to synonymy. A new species was also described. The criterion used by Wright (1915) to delimit the two genera was the position of the flowers: 'Flowers axillary, solitary' in *Cryptadenia* opposed to 'Flowers terminal, capitate, rarely solitary' in *Lachnaea*. At present *Cryptadenia* is considered to comprise five species (Van Wyk 1993).

Both *Lachnaea* and *Cryptadenia* are endemic to the Cape Province. *Lachnaea* is found mainly at high altitudes from Clanwilliam in the north to the Cape Peninsula in the south and eastwards along the coastal areas as far as Uitenhage. Further inland it occurs on the mountain ranges from Ceres through Worcester to Ladismith (Bond & Goldblatt 1984). The centre of diversity is in the southwestern area. *Cryptadenia* occurs on sandy flats and lower mountain slopes from Piketberg in the west to the Cape Peninsula, and along the coastal areas to Bredasdorp and inland to Ceres (Bond & Goldblatt 1984).

Lachnaea and its closest related genus, *Cryptadenia*, are both characterized by the absence of petals and by a hypanthium having scales below the insertion of the stamens. Beyers & Van der Walt (1994), contrary to Wright (1915), found that the two genera could not be distinguished on the inflorescence structure. With the large number of herbarium specimens now available, compared to the small range of material on which earlier studies were based, a sound delimitation of the two genera is possible. The aim of the present investigation was to compare the two genera using a multidisciplinary approach, with the view to establishing whether they are congeneric

or not. Besides the morphological study accompanied by field work, anatomical, palynological and karyological investigations were undertaken to assess the taxonomic value of the evidence derived from these sources.

MATERIALS AND METHODS

Eighteen taxa were selected, 14 from *Lachnaea* and four from *Cryptadenia*. The aim in selecting the taxa was to have as broad a representation as possible of all the taxa in the two genera. The criteria used for selecting the *Lachnaea* taxa were as follows: a, taxa representative of the three sections instituted by Meisner (1840), taking into account the variation in each section; b, all taxa with solitary flowers; c, the position of the scales in the floral tube; d, the stigma types; e, the degree of asymmetry of the calyx lobes.

Wright's revision of *Lachnaea* and *Cryptadenia* in *Flora capensis* (1915 and 1925) was followed. Type specimens and quoted specimens were examined to verify the species concepts for the taxa used in this study. Infraspecific variation has been included in each taxon studied and has not been treated individually.

Four of the five species of *Cryptadenia* currently recognized were studied. *Cryptadenia breviflora* Meisn. was excluded as it is an intermediate taxon between *Cryptadenia grandiflora* (L. f.) Meisn. and *Cryptadenia uniflora* Meisn., which Levyns (1950) considered to be a hybrid between these two species.

The following species were studied: *Lachnaea aurea* Eckl. & Zeyh., *L. axillaris* Meisn., *L. burchellii* Meisn., *L. buxifolia* Lam., *L. capitata* (L.) Meisn., *L. densiflora* Meisn., *L. diosmoides* Meisn., *L. ericoides* Meisn., *L. eriocephala* L., *L. filamentosa* (Thunb.) Meisn., *L. nervosa* Meisn., *L. penicillata* Meisn., *L. ruscifolia* Compton, *Cryptadenia filicaulis* Meisn., *C. grandiflora*, *C. laxa* C.H. Wright and *C. uniflora* (author citations according to Van Wyk 1993).

For the anatomical study of the foliage leaves, both material preserved in FAA and herbarium material was used. The herbarium material was soaked in 50% ethanol for 24 hours, thereafter treated as preserved material. The preserved material was dehydrated and embedded in wax according to the tertiary butyl method (Johansen 1940). Transverse sections 12 μm thick were made through the middle of the leaf blade with the aid of a rotary microtome and stained with Alcian Green Safranin (AGS) (Joel 1983). Scanning electron micrographs of the leaf surfaces were obtained by mounting portions from the same region of the leaf blade of herbarium material on stubs which were coated with gold and studied with a Joel JSM-35 scanning electron microscope. Epidermal cell patterns of the leaf blade were studied under a light microscope after the adaxial and abaxial epidermal layers were peeled off and mounted in water.

The anatomical study of the flowers was done on material preserved in FAA. The preserved material was dehydrated and embedded in wax according to the tertiary butyl method (Johansen 1940). For the anatomy, transverse

Species	Voucher specimens	Leaf anatomy	Floral anatomy	Pollen morph.	Karyology
aurea	*Beyers 135* (STE)	×		×	
axillaris	*Beyers 127, 180* (STE)	×	×		
	Beyers 197 (STE)		×		
	Schlechter 7702 (BOL)	×			
	Steyn 331 (NBG)			×	
burchellii	*Oliver 9241* (STE)	×		×	
	Oliver 9251 (STE)	×			
buxifolia	*Beyers 118* (STE)		×	×	
	Beyers 122 (STE)	×		×	
	Taylor 8648 (STE)			×	
capitata	*Beyers 128* (STE)		×	×	
	Beyers 138 (STE)	×			
	Hugo 231 (STE)			×	
densiflora	*Beyers 115* (STE)	×		×	
	Beyers 117 (STE)			×	
	Beyers 145 (STE)	×		×	×
	Beyers 171 (STE)	×			
	Beyers 177 (STE)	×			
diosmoides	*Beyers 181* (STE)	×	×	×	×
	Spreeth 158 (STE)	×			
	Van Niekerk 53 (BOL)			×	
ericoides	*Beyers 172* (STE)	×			×
	McDonald 1842 (STE)			×	
	Zeyher 3776 (SAM)			×	
eriocephala	*Beyers 54* (STE)	×	×	×	×
	Spreeth 141 (STE)			×	
filamentosa	*Beyers 110* (STE)	×		×	
	Taylor 10770 (STE)			×	
funicaulis	*Beyers 125* (STE)	×		×	
	Du Toit s.n. (STE)				×
nervosa	*De Kock 152* (STE)	×		×	
penicillata	*Beyers 173* (STE)	×		×	
	McDonald 16321 (STE)			×	
	Oliver & Fellingham 9145 (STE)			×	
ruscifolia	*Beyers 193* (STE)	×			
	Goldblatt & Manning 8870 (STE)	×			
	Vlok 2084 (STE)	×	×	×	

sections were used almost exclusively and longitudinal sections were resorted to only to verify the points of attachment of the floral structures. Serial sections were cut 12 μm in thickness. AGS staining (Joel 1983) as well as Crystal Violet and Erythrosin staining (Jackson 1926) were used. The AGS staining technique was found to give better results.

Pollen was taken from herbarium specimens and from material collected in the wild. For both light microscopy (LM) and scanning electron microscopy (SEM), pollen was acetolyzed according to Erdtman (1960). Acetolyzed samples were prepared for both SEM and LM according to the method of Marais (1990). At least 20 pollen grains of each taxon were measured. Transverse sections ± 15 μm thick were made with the aid of a freeze-microtome to study the structure of the pollen wall of two taxa in

each genus. The terminology used to describe the pollen morphology is that of Walker & Doyle (1975).

For chromosome studies inflorescences were fixed in Carnoy's fixative in the field. After 24 hours, the fixative was replaced with 85% ethanol for 15 minutes and then finally replaced with 70% ethanol. Flower buds were stained in Snow's fluid (1963). The anthers were removed and squashed in 45% acetic acid.

Voucher specimens for the anatomy of leaves and flowers and for pollen morphology and karyology are given in Tables 1 and 2.

RESULTS

Habit

In *Lachnaea* the species are sparsely to densely branched, erect shrubs or erect to sprawling shrublets 0.15–2.00 m high. There is considerable variation in appearance and size among, and sometimes within species. The *Cryptadenia* species are erect or sprawling, moderately to densely branched shrublets 0.12–0.80 m high. In both genera the species are either basally single-stemmed, multi-stemmed, or single-stemmed and multi-stemmed within a single species. The branches are leafy, usually with an adpressed pubescence, later becoming naked and glabrous, and usually marked with the leaf scars of the fallen leaves.

Morphology of foliage leaves

In *Lachnaea* the leaves are alternate or decussate, but in *L. burchellii* they are opposite or subopposite and in *L. diosmoides* they are alternate to subopposite. The leaves are adpressed, ascending, patent or occasionally reflexed, and imbricate to scattered. The leaves in *Cryptadenia* are decussate, adpressed, ascending or sub-patent, and imbricate or scattered. In both genera the orientation and position of the leaves on the axis may vary inter- and intraspecifically.

Species	Voucher specimens	Leaf anatomy	Floral anatomy	Pollen morph.	Karyology
filicaulis	*Boucher 5071* (STE)	×	×		
	Esterhuysen 34370 (BOL)			×	
	McDonald 1989 (STE)				×
	Oliver 9803 (STE)	×	×		
grandiflora	*Beyers 129, 151* (STE)	×		×	
	Beyers 196 (STE)		×		
laxa	*Bolus 7875* (BOL)	×		×	
	I. Oliver 4 (STE)	×	×		
uniflora	*Beyers 136* (STE)	×	×	×	×
	Haynes 447 (STE)			×	

The leaves in both genera are always entire and usually sessile except in *L. ruscifolia* where they may be sub-petiolate. The shape of the leaves in *Lachnaea* can be linear-elliptic to elliptic, oblanceolate, obovate or ovate (Figures 1, 2). Again, the variability is not only among the species but may be within a particular species (Figure 2). The leaves range in size from 2–34 × 0.6–9.0 mm. Within some species, as in *L. filamentosa* (Figure 2), the variation in leaf size may be considerable, namely from 5–34 × 1.8–12.0 mm. In *Cryptadenia* the shape of the leaves can be lanceolate, narrowly elliptic, narrowly ovate or obovate. In *C. uniflora* the leaves are always narrowly elliptic but in *C. grandiflora* they are narrowly elliptic, narrowly obovate, obovate or oblanceolate. As in *Lach-naea* the shape and size of the leaves vary inter- and in-traspecifically (Figure 3). The range in leaf size is 2.9–12.8 × 0.6–3.2 mm. The leaves in both genera are coriaceous but in *L. densiflora* they are occasionally semi-succulent.

In *Lachnaea* the abaxial side of the leaves may be flat, obtusely convex to convex, or faintly keeled or keeled in the distal half. Adaxially they may be flat, obtusely con-cave or concave. Both surfaces of the leaves are usually smooth. However, the abaxial surface in *L. ruscifolia* and *L. nervosa* has several longitudinal ribs, whereas in *L. diosmoides* there is only a single midrib. The abaxial sur-face is usually green and shiny, whereas the adaxial sur-face is usually pale green, dull and white-punctulate but in some species the leaves are concolorous. The con-
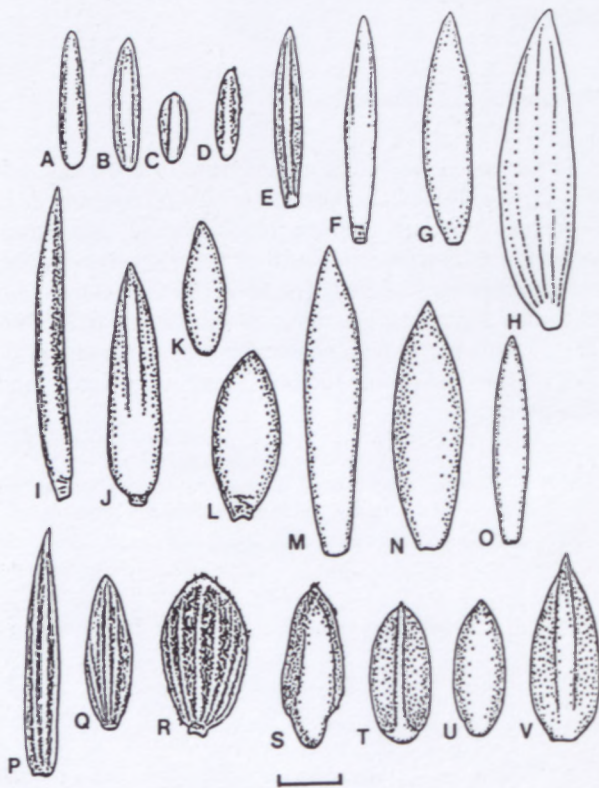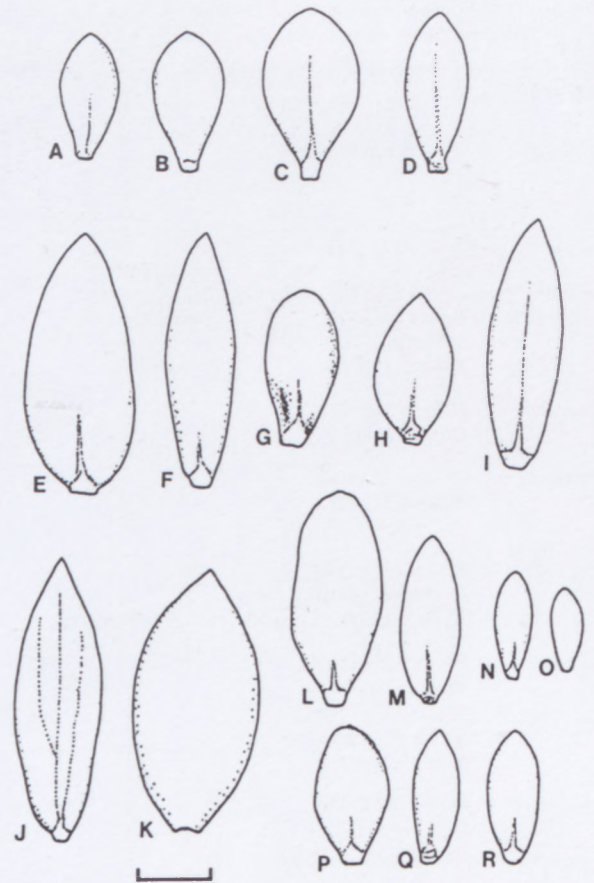

FIGURE 2.—*Lachnaea buxifolia* and *L. filamentosa*. Variation in leaf shape and size, abaxial view. A–I, *L. buxifolia*: A–C, *McDonald 1683*; D, *Marais s.n.*; E–G, *Beyers 118*; H & I, *Beyers 122*. J–R, *L. filamentosa*: J & K, *Low 1246*; L & M, *Beyers 109*; N & O, *Beyers 118*; P–R, *Taylor 12001*. Scale bar: 6 mm.

colorous leaves are usually green but in *L. buxifolia*, and sometimes in *L. filamentosa*, they are glaucous. In *Cryp-tadenia* the abaxial side of the leaves is convex, faintly

FIGURE 1.—*Lachnaea*. Variation of leaf shape and size, abaxial view. A, *L. eriocephala, Beyers 54*; B & C, *L. ericoides, Beyers 172*; D, *L. funicaulis, Beyers 125*; E, *L. diosmoides, Beyers 181*; F, *L. capitata, Beyers 128*. G & H, *L. burchellii*: G, *Oliver 9251*; H, *Spreeth 155*. I–L, *L. densiflora*: I & J, *Oliver 9129*; K, *Taylor 12023*; L, *Beyers 171*. M–O, *L. aurea, Beyers 135*; P & Q, *L. nervosa, De Kock 152*; R, *L. ruscifolia, Beyers 193*; S, *L. penicillata, Beyers 173*. T–V, *L. axillaris*: T, *McDonald 1395*; U & V, *Beyers 197*. Scale bars: A–R, 3 mm; S–V, 1 mm.
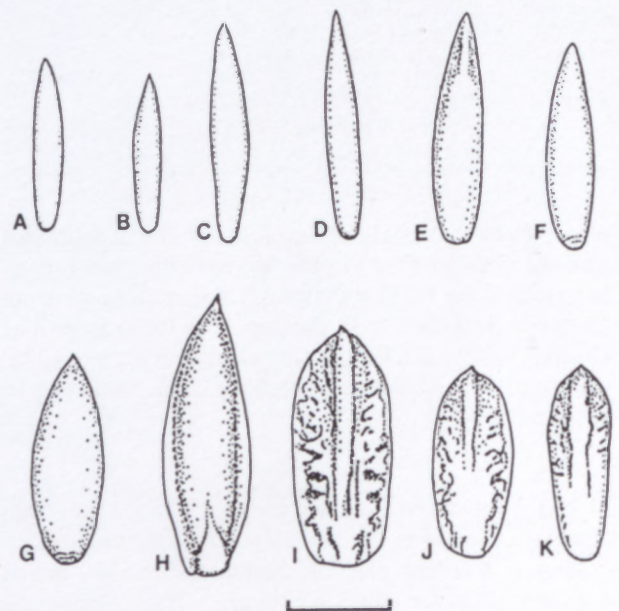

FIGURE 3.—*Cryptadenia*. Variation in leaf shape and size, abaxial view. A–C, *C. filicaulis*: A, *McDonald 1988*; B & C, *Oliver 9803*. D, *C. uniflora, Beyers 136*; E & F, *C. laxa, I. Oliver 4*. G–K, *C. grandiflora*: G, *Beyers 136*; H, *Vlok 2179*; I–K, *Beyers 129*. Scale bar: 3 mm.
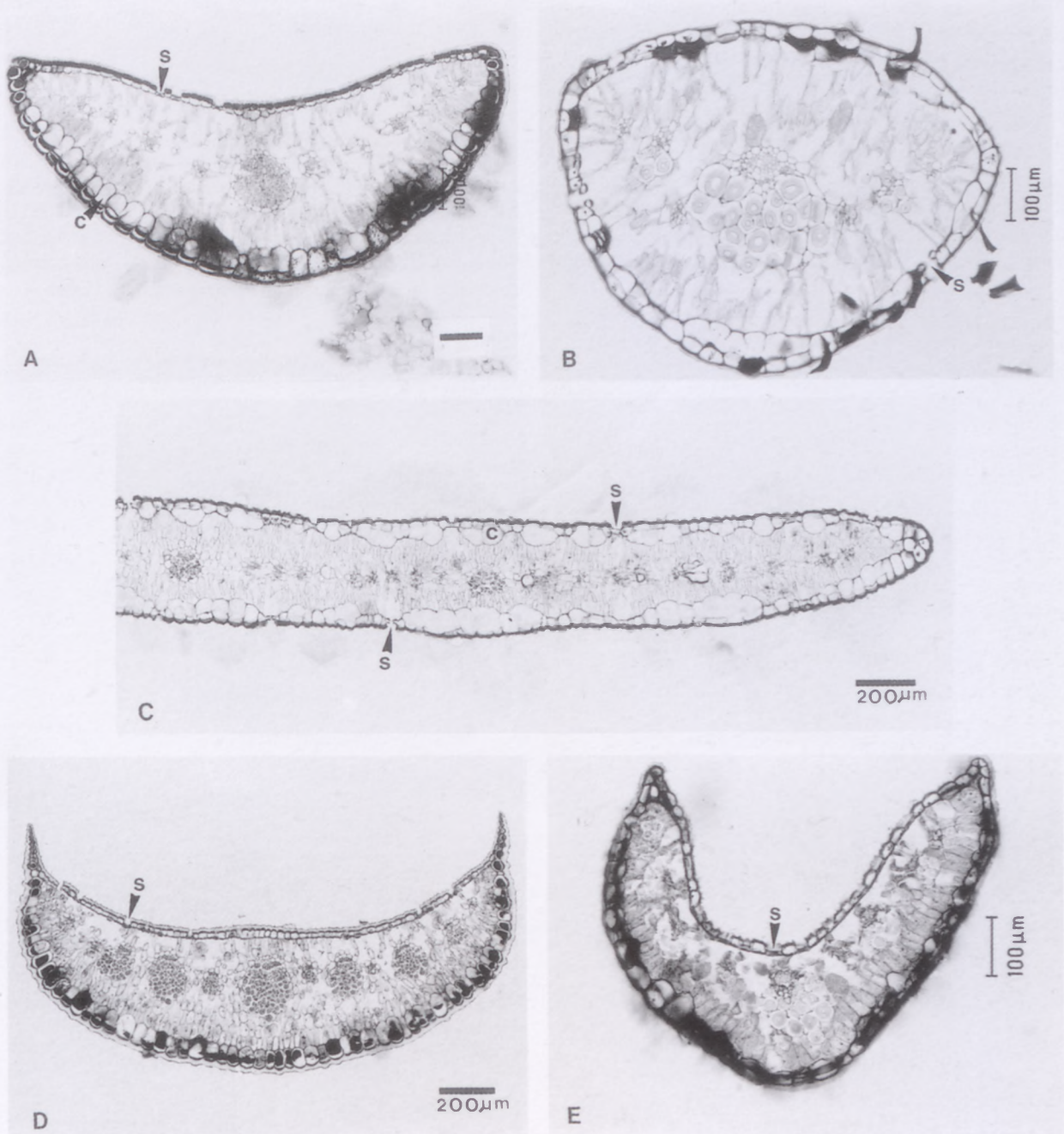
FIGURE 4.—*Lachnaea* and *Cryptadenia*. Leaf transections, adaxial face above. A, *L. eriocephala, Beyers 54*; B, *L. densiflora, Beyers 115*; C, *L. buxifolia, Beyers 122*; D, *C. grandiflora, Beyers 151*; E, *C. laxa, 1.Oliver 4*. c, large cells of inner layer of biseriate epidermis; s, stoma. Scale bars: A, B, E, 100 µm; C, D, 200 µm.

keeled or keeled, smooth or transversely rugulose towards the margins with a shiny, green surface, whereas adaxially they are concave with a smooth, dull, pale green, white-punctulate surface.

In *Lachnaea* the leaves are glabrous or pubescent at the margins but the marginal pubescence is often deciduous, whereas in *Cryptadenia* the leaves are always glabrous.

Anatomy of foliage leaves

In transverse sections the leaves of most *Lachnaea* species and all *Cryptadenia* species appear concave adaxially and convex abaxially (Figure 4A, D, E), but in

L. densiflora both surfaces are flat or the adaxial one may be slightly convex (Figure 4B); in *L. buxifolia* (Figure 4C) and *L. filamentosa* both surfaces are flat.

Cuticle

In *Lachnaea* the cuticle is well developed and of even thickness on both sides, or thicker on the abaxial side, whereas in *Cryptadenia* the well-developed cuticle is always thicker abaxially. Under the SEM the adaxial and abaxial cuticles of the *Lachnaea* species are unsculptured (Figure 5A, D), undulate (Figure 5B, E) or minutely papillate (Figure 5C, F). In *Cryptadenia* the cuticle is usually minutely papillate adaxially, as in *C. grandiflora* (Figure 6A), but in *C. filicaulis* it is unsculptured (Figure 6B). The relief of the

abaxial cuticle is either minutely papillate (Figure 6C) or undulate (Figure 6D). In *C. grandiflora*, however, both types of cuticular sculpturing occur abaxially.

Waxes in the form of small flakes occur commonly on the adaxial leaf surfaces of *Cryptadenia* species and most *Lachnaea* species (Figure 7A, C). In both genera, when waxes are present on the abaxial surface, they are sparse and flakelike (Figure 7B, D). Cutter (1978) is of the opinion that it is this wax deposit that gives the 'bloom' to glaucous leaves.

Trichomes, when present, are non-glandular and uniseriate in both genera.

Epidermis

In both genera the adaxial epidermis is composed of small cells with thin anticlinal and inner tangential walls and slightly thicker outer tangential cell walls. In *L. eriocephala* the outer tangential cell walls are the thickest (Figure 4A). In *Lachnaea* and *Cryptadenia* the adaxial epidermis is uniseriate as in *L. eriocephala* (Figure 4A)

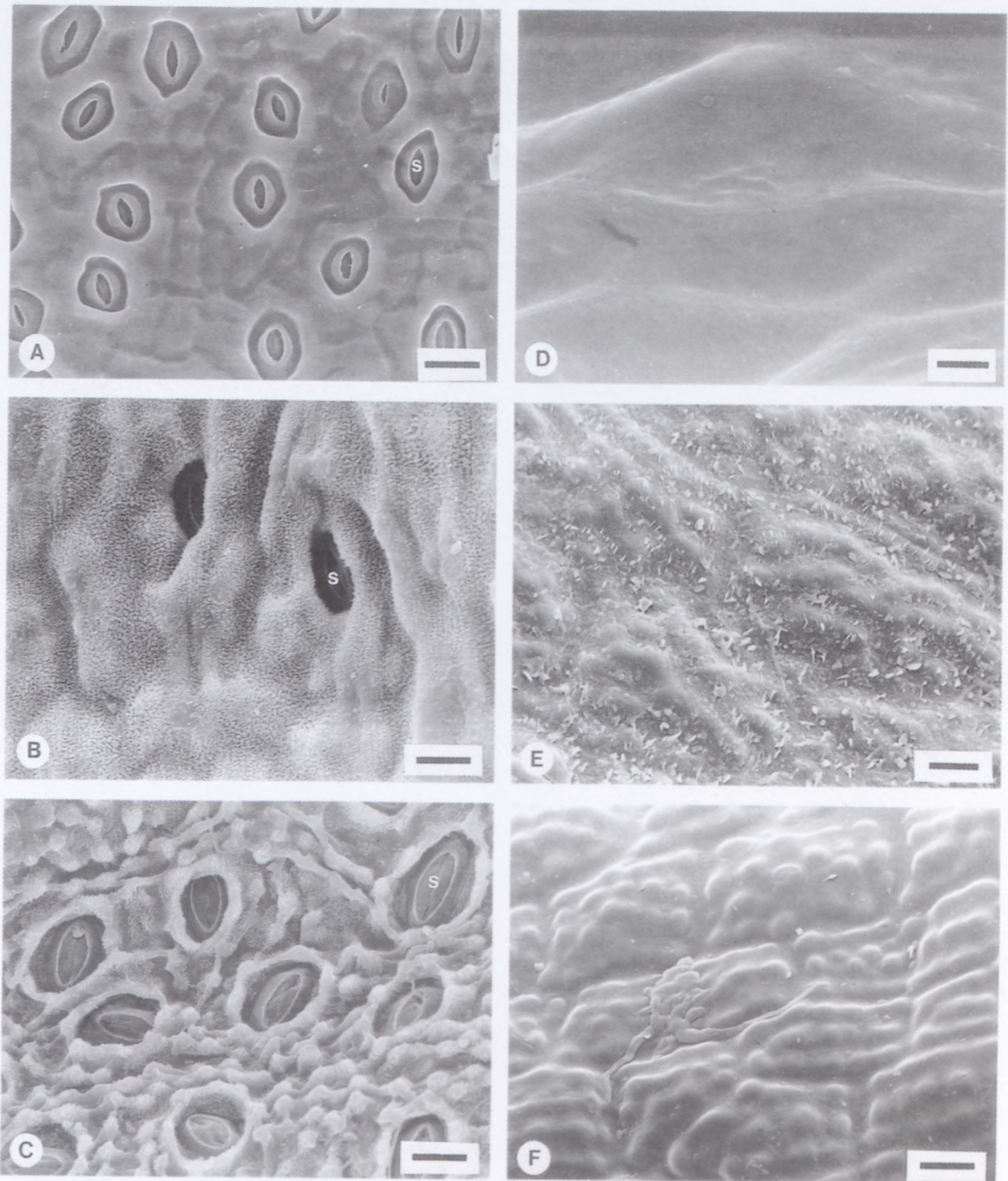FIGURE 5.—*Lachnaea*. SEM micrographs of cuticular relief of leaf. A–C, adaxial surface: A, *L. funicaulis, Beyers 125*, smooth; B, *L. buxifolia, Beyers 122*, undulate; C, *L. ericoides, Beyers 172*, minutely papillate. D–F, abaxial surface: D, *L. ericoides, Beyers 172*, smooth; E, *L. diosmoides, Beyers 181*, undulate; F, *L. funicaulis, Beyers 125*, minutely papillate. s, stoma. Scale bars: A–F, 20 μm.
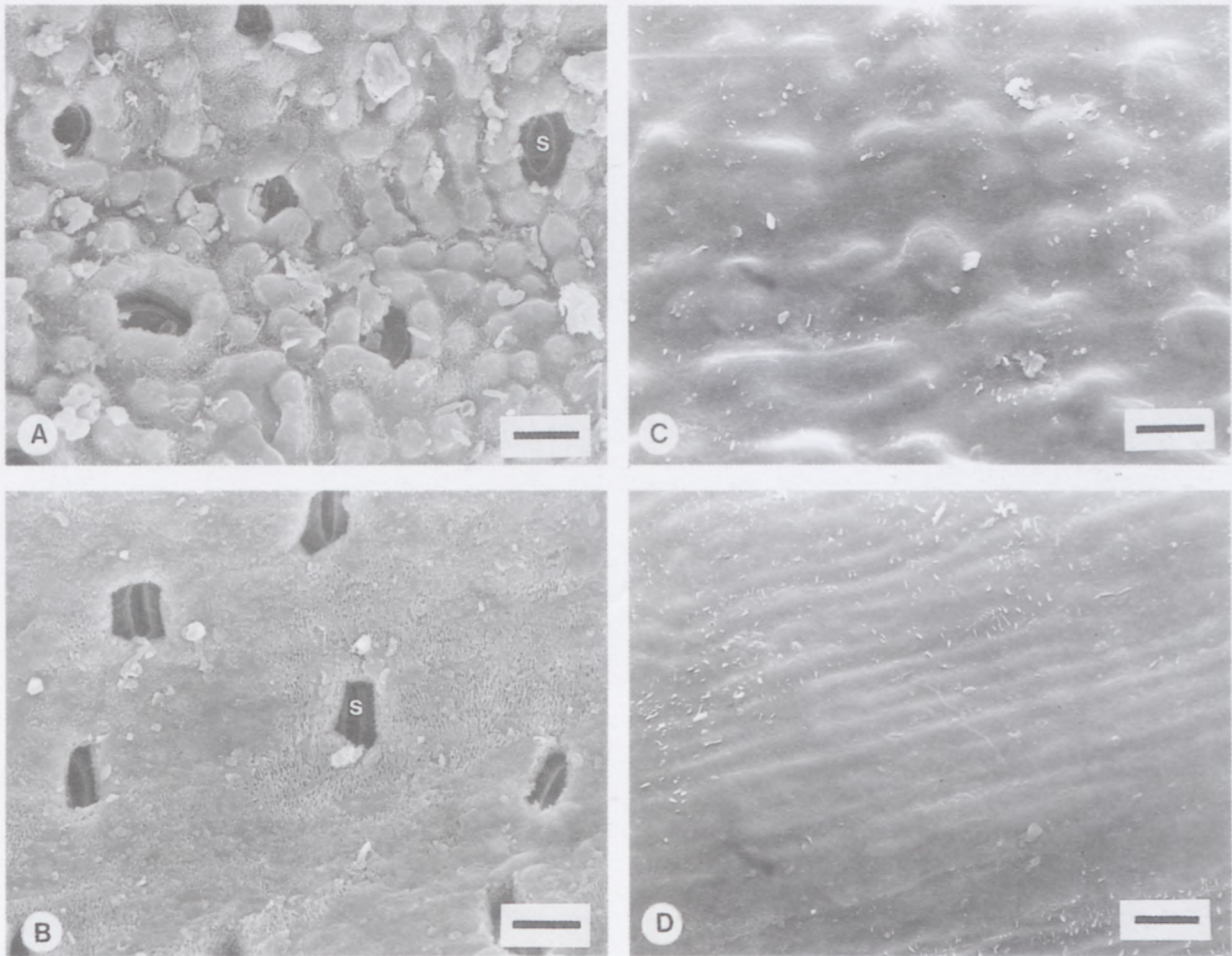
FIGURE 6.—*Cryptadenia*. SEM micrographs of cuticular relief of leaf. A, B, adaxial surface: A, *C. grandiflora*, *Beyers 129*, minutely papillate; B, *C. filicaulis*, *Boucher 5071*, smooth. C, D, abaxial surface: C, *C. grandiflora*, *Beyers 129*, minutely papillate; D, *C. filicaulis*, *Boucher 5071*, undulate. s, stoma. Scale bars: A–D, 20 μm.

and *C. grandiflora* (Figure 8D, E), incompletely uniseriate (occasional cells with periclinal walls) as in *L. ericoides* (Figure 8A) and *C. uniflora* (Figure 8C), incompletely biseriate (occasional cells without periclinal walls) as in *L. densiflora* (Figure 4B) and *C. laxa* (Figure 4E) or biseriate as in *L. buxifolia* (Figure 4C). The abaxial epidermis is usually biseriate in both genera. However, in *L. axillaris* and *L. ericoides* (Figure 8A) it is incompletely biseriate and in *C. grandiflora* it may be uniseriate (Figure 8D) or incompletely biseriate (Figure 8E).

When the epidermis is biseriate, the cells of the inner layer are usually larger than those of the outer layer. The epidermis contains mucilage, except in *C. grandiflora* where it was not always observed. The mucilage may be present in the cells of the inner and outer epidermal layers, or in the cells of the inner layer only.

Tannin occurs in the epidermis of *L. axillaris*, *L. burchellii*, *L. diosmoides*, *L. ericoides*, *L. funicaulis*, *L. penicillata*, *C. grandiflora* and *C. uniflora*.

Druse crystals were observed in the epidermis of *L. buxifolia*, *L. filamentosa* and *L. ruscifolia*, and sometimes in the adaxial epidermis of *C. grandiflora*.

Stomata

The stomata in both genera are anomocytic and sunken except in *L. funicaulis* and *L. penicillata* where they are on the same level as the outer walls of the surrounding epidermal cells. In *Lachnaea* the leaves are epistomatic or amphistomatic but in *Cryptadenia* they are only epistomatic. When the leaves are amphistomatic, there are usually more stomata adaxially.

Mesophyll

In both genera the cells of the mesophyll are chlorenchymatous and palisade-like (elongated perpendicular to the axis) with the exception of *C. grandiflora* where they are either palisade-like (Figure 8E) or short and more or less round (Figure 8D). As a result of the size of the intercellular spaces, the leaves can be classified as dorsiventral or isobilateral. When dorsiventral, the smaller intercellular spaces occur abaxially and the larger ones adaxially as in *L. axillaris*, *L. diosmoides* (Figure 8B), *L. ericoides*, *L. eriocephala*, *L. funicaulis*, *L. nervosa*, *L. penicillata*, *C. filicaulis*, *C. laxa* and *C. uniflora* (Figure 8C). The isobilateral arrangement occurs in *L. aurea*, *L. burchellii*, *L. buxifolia*, *L. capitata*, *L. densiflora* (Figure 4B), *L. filamentosa* and *L. ruscifolia*. In *C. grandiflora*

however, a dorsiventral or an almost isobilateral arrangement is found.

Tannin occurs in the parenchymatous cells surrounding the median vascular bundle in *L. penicillata* and sometimes in the mesophyll in *C. grandiflora*.

Druse crystals are present in the mesophyll of *L. aurea, L. axillaris, L. burchellii, L. buxifolia, L. capitata, L. densiflora, L. filamentosa, L. nervosa* and the four *Cryptadenia* species, and in the vascular tissue of *L. filamentosa*.

Venation and vascular bundles

The venation in both genera is reticulate and the vascular bundles are collateral. As Metcalfe & Chalk (1950) stated, no internal phloem occurs in the midrib.

In both genera, extraxylary fibres occur abaxially in association with the vascular bundles. A prominent median fibre strand (Figure 8) is present in all the species except in *L. buxifolia* and *L. filamentosa*. In addition to the prominent median fibre strand, equally prominent fibre strands occur in association with the larger lateral vascular bundles in *L. nervosa, L. ruscifolia* and *C. grandiflora* (Figure 8E). In *L. ruscifolia* the median and larger lateral strands extend to the abaxial epidermis.

Extraxylary fibres not associated with the vascular bundles, occur along the lateral margins immediately below the epidermis in *L. aurea* (Figure 8F).

Morphology of flower and fruit

Pedicel/floral articulation

The flowers in *Lachnaea* are either sessile or shortly pedicellate with pedicels up to 2.5 mm long. In *Cryptadenia* the flowers are always sessile. In *L. eriocephala, L. funiculis* and *L. penicillata* the sericeous to villous pedicels elongate in the fruiting stage and remain on the plant long after the fruit has been shed. These hairy pedicels are responsible for the woolly appearance of the old inflorescences. The flowers of *Lachnaea* and *Cryptadenia* are at their bases surrounded by a ring of trichomes, which occurs at the floral articulation of the sessile flowers or on the pedicels.

Hypanthium

In *Lachnaea* the basal portion of the hypanthium is ellipsoid to widely ellipsoid, ovoid to widely ovoid, or obovoid, whereas the portion above the plane of circumscision is funnel-shaped, cylindrical, obconical, cup-shaped or cup-shaped with a sigmoid curve at the base (Figure 9). In *Cryptadenia* the basal portion of the hypan-

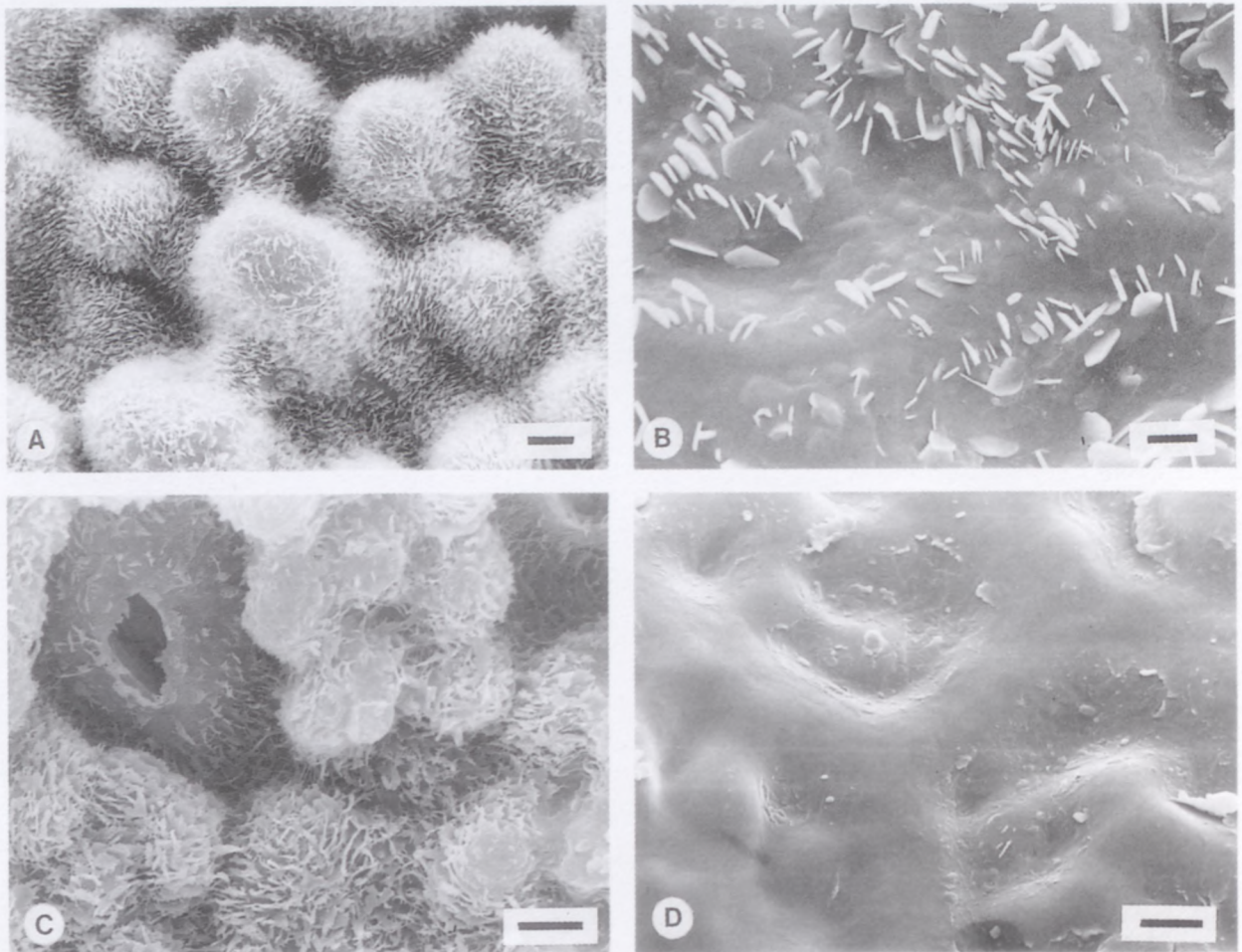FIGURE 7.—*Lachnaea* and *Cryptadenia.* SEM micrographs of flaky surface wax on leaf. A, B, *L. aurea, Beyers 135*: A, adaxial surface; B, abaxial surface. C, D, *C. laxa, Bolus 7875*: C, adaxial surface; D, abaxial surface. Scale bars: A–D, 5 μm.
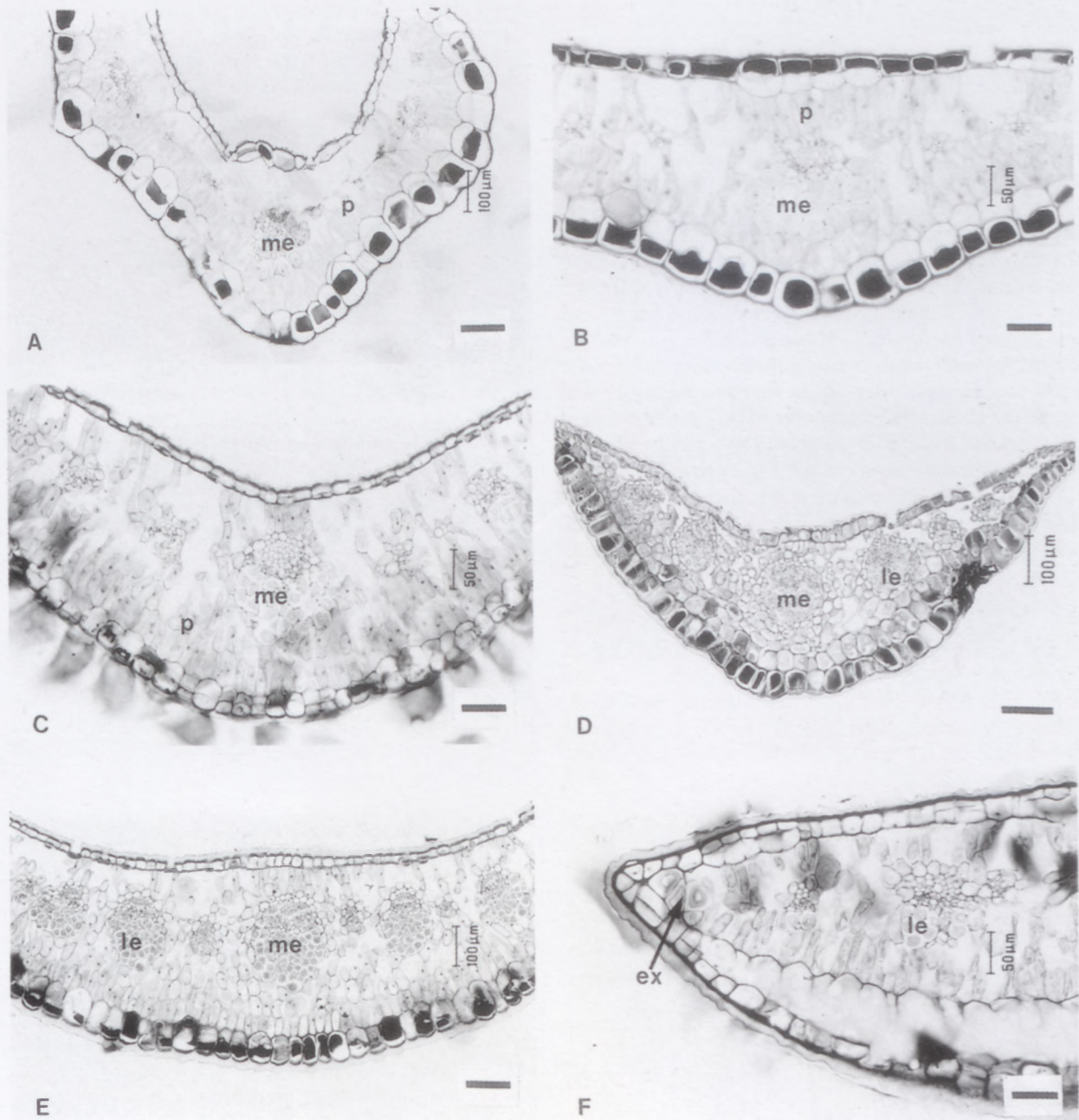
FIGURE 8.—*Lachnaea* and *Cryptadenia*. Leaf transections, adaxial face above. A–E, median vascular bundle: A, *L. ericoides, Beyers 172*; B, *L. diosmoides, Beyers 181*; C, *C. uniflora, Beyers 136*; D, *C. grandiflora, Beyers 129*; E, *C. grandiflora, Beyers 151*. F, leaf margin of *L. aurea, Beyers 54*, showing extraxylary fibres (ex) along lateral margin. p, palisade-like chlorenchyma; me, median extraxylary fibre strand; le, lateral extraxylary fibre strand. Scale bars: A, D, E, 100 μm; B, C, F, 50 μm.

thium is ovoid or ellipsoid, whereas the upper portion above the plane of circumscision is funnel-shaped or cup-shaped (Figure 9). The position of the plane of circumscision, expressed as a percentage of the length of the base to the total length of the hypanthium, varies from 20–80% in both genera. The upper portion of the hypanthium abscises soon after seedset at the plane of circumscision. The length of the hypanthium ranges from 1.5–17.5 mm in *Lachnaea* and from 2.2–11.0 mm in *Cryptadenia*.

The outer surface of the base of the hypanthium is pubescent or glabrous in *Lachnaea* and pubescent in *Cryptadenia*, whereas the inner surface is usually glabrous in both genera, except in *L. buxifolia* and *C. uniflora* where it is pubescent. The outer and inner surfaces of the

upper portion of the hypanthium in both genera are usually pubescent, but in *L. axillaris* the outer surface is glabrous.

In both genera the shape of the trichomes and type of pubescence on the outer surface of the hypanthium often changes around the plane of circumscision. In *L. burchellii* the trichomes on the basal portion are clavate, whereas those on the upper portion are longer and acicular (Figure 10). In *C. laxa* the trichomes of the basal portion are obtuse, whereas those of the upper portion are acicular. The pubescence on the outer surface of the hypanthium is denser in the vicinity of the scales in both *Lachnaea* and *Cryptadenia*. The upper portion of the hypanthium and the calyx are concolorous.

Calyx

The calyx in both genera comprises four sepals which are fused to the rim of the hypanthium. In *Lachnaea* the sepals vary from being almost equal to distinctly unequal, but with a gradual transition from one form to the other (Figure 11). In the distinctly zygomorphic forms the anterior lobe is usually the longest. The sepals are narrowly to widely elliptic, ovate to widely ovate, or obovate to widely obovate. The size of the anterior sepal ranges from 1.3–22.0×0.8–7.5 mm, that of the two lateral sepals from 1.3–7.5×0.6–4.5 mm, and that of the posterior sepal from 1.2–5.5×0.7–3.5 mm. Because the flowers of *L. axillaris* and *L. ruscifolia* are solitary, the outer sepals represent the posterior and anterior sepals and the two inner sepals represent the two lateral sepals. The abaxial surface of the sepals is pubescent, except in *L. axillaris* where it is glabrous. The adaxial surface of the sepals is usually pubescent, but in *L. aurea* and *L. nervosa* it is glabrous and in *L. axillaris* and *L. funicaulis* it is partly glabrous and partly pubescent. The calyx is white, cream, pink, pale blue, white or cream tinged with pink or blue, or yellow.

The sepals in *Cryptadenia* are almost equal (Figure 12), narrowly to widely elliptic, ovate or orbicular, varying in size from 1.6–10.7×1.2–5.8 mm with the apices acute, rounded or obtuse. The abaxial surface is pubescent whereas the adaxial surface is either glabrous or pubes-

FIGURE 10.—*Lachnaea burchellii, Oliver 9241.* SEM micrograph of trichome structure on outer surface of hypanthium around circumscision zone. b, basal portion of hypanthium; c, plane of circumscision; u, upper portion of hypanthium. Scale bar: 200 µm.

cent. The calyx is white, cream, white tinged with pink, pink or mauve-pink.

The aestivation of the sepals is decussate-imbricate in *Lachnaea* and *Cryptadenia.*

Petals

Petals are absent in all taxa.

Androecium

Eight stamens in two whorls of four are present in all taxa. In *Lachnaea* the outer whorl, the antisepalous stamens, are episepalous, inserted on the basal portion of the sepals, or they are inserted on the rim of the hypanthium (Figure 11). The stamens of the inner whorl, the antipetalous stamens, are inserted on or very close to the rim of the hypanthium or a third of the way down the throat of the upper portion of the hypanthium as in *L. capitata* (Figure 11F).

In *Cryptadenia* the outer whorl, the antisepalous stamens, are episepalous, fused to the basal portion of the sepals as in *C. grandiflora* and *C. laxa,* or inserted in the upper throat of the hypanthium as in *C. uniflora* and *C. filicaulis* (Figure 12). The inner whorl, the antipetalous stamens, are inserted at the rim of the hypanthium in *C. laxa,* a quarter of the way down in the upper portion of the hypanthium in *C. uniflora* and a third of the way down in *C. filicaulis* and *C. grandiflora* (Figure 12). The stamens are fully exserted in *Lachnaea* (Figure 11). In *Cryptadenia* the antisepalous stamens of all the taxa and the antipetalous stamens of *C. laxa* are exserted. In the other *Cryptadenia* species only the anthers of the antipetalous stamens are exserted or semi-exserted (Figure 12).

The anthers are basifixed and introrse. In *Lachnaea* they are either spherical or oblate-spherical, whereas in *Cryptadenia* they are ellipsoid or ovoid.
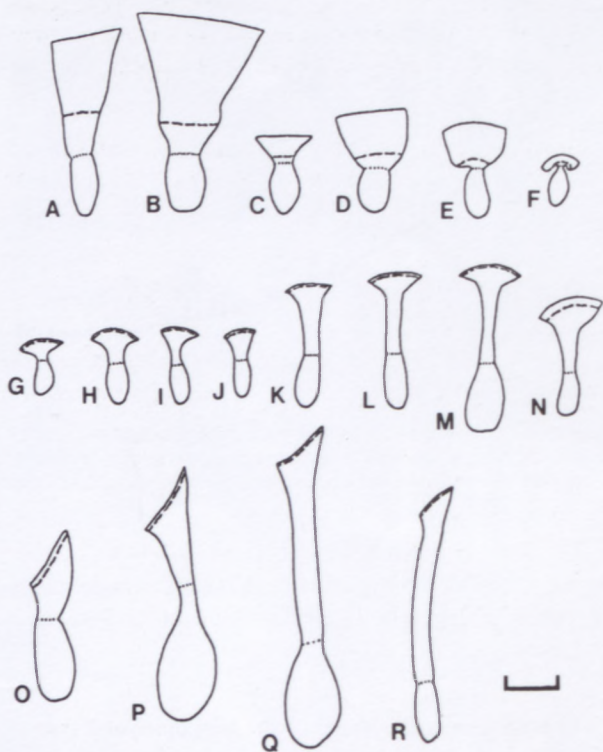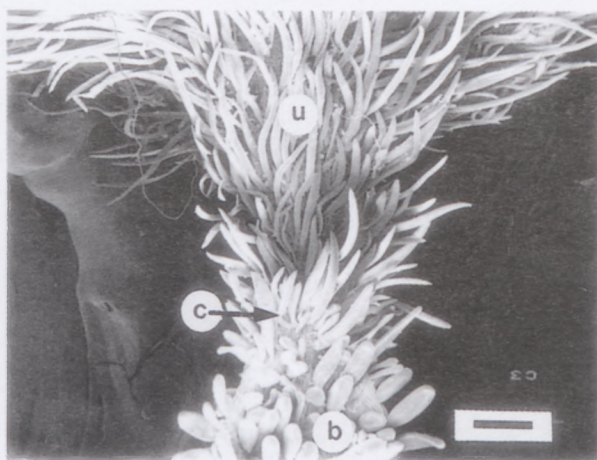

FIGURE 9.—*Lachnaea* and *Cryptadenia.* Hypanthia, showing plane of circumscision, lower dotted line; and scales, upper dashed line. A, *C. uniflora, Beyers 136*; B, *C. grandiflora, Beyers 129*; C, *L. densiflora, Oliver 9129*; D, *L. capitata, Beyers 138*; E, *C. filicaulis, Thompson 3789*; F, *L. axillaris, Bolus 8596*; G, *L. ericoides, Beyers 172*; H, *L. burchellii, Oliver 9241*; I, *L. funicaulis, Beyers 125*; J, *L. penicillata, Beyers 173*; K, *L. ruscifolia, Vlok 2084*; L, *C. laxa, Bolus 7875*; M, *L. nervosa, De Kock 152*; N, *L. diosmoides, Compton 7580*; O, *L. aurea, Beyers 135*; P, *L. filamentosa, Beyers 110*; Q, *L. buxifolia, Beyers 118*; R, *L. eriocephala, Beyers 54.* Scale bar: 2 mm.
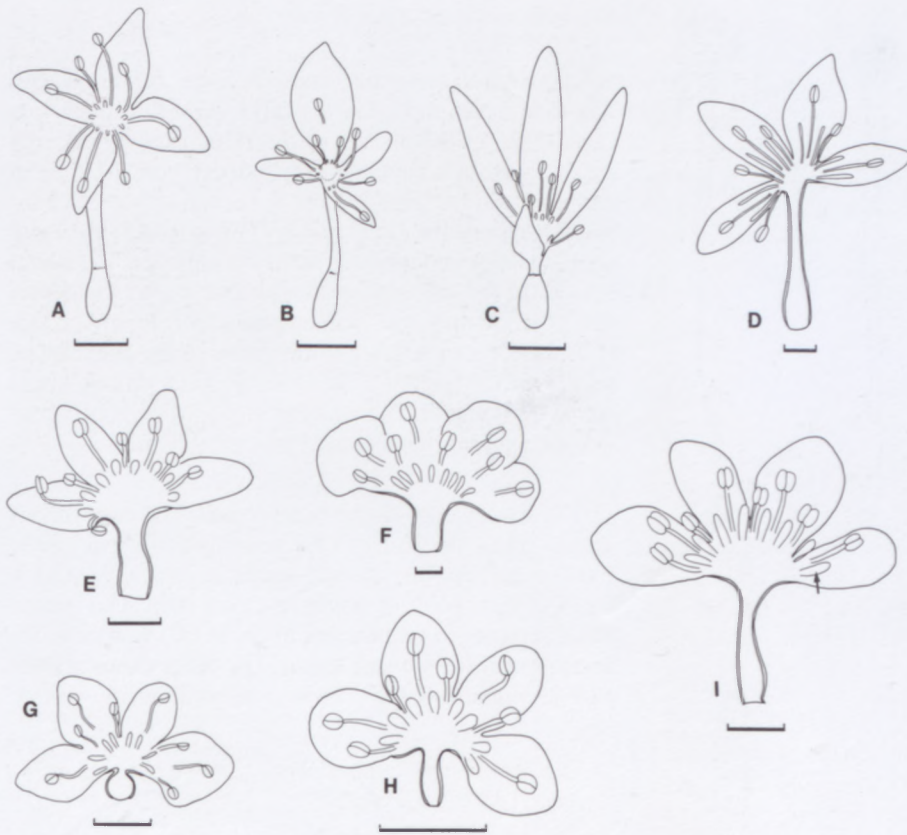
FIGURE 11.—*Lachnaea*. Flowers. A, *L. buxifolia, Beyers 122*; B, *L. filamentosa, Kruger 977*; C, *L. aurea, Gillett 4343*; D, *L. nervosa, De Kock 152*; E, *L. funicaulis, Marsh 758*; F, *L. capitata, Beyers 138*; G, *L. densiflora, Boucher 1767*; H, *L. ericoides, McDonald 2027*; I, *L. penicillata, Oliver & Fellingham 9145*. D–I: flowers split longitudinally with gynoecia removed; floral scales (arrow in I) shown in each flower below stamens. Scale bars: A–C, 4 mm; D–I, 2 mm.

Scales

Eight scales are inserted on the upper portion of the hypanthium below the attachment of the antipetalous stamens and alternating with the stamens. The position of the scales varies in different species of both genera. In most *Lachnaea* species the scales are inserted at the mouth of the hypanthium but in some species they are inserted two thirds or halfway down the upper portion of the hypanthium (Figure 11). In *Cryptadenia* they are inserted either at the mouth of the hypanthium or from midway to three quarters of the way down the upper portion of the hypanthium (Figure 12).

The shape of the scales varies in the different taxa. They can be linear, clavate, subrotund, capitate, ovoid or obovoid in *Lachnaea*, whereas in *Cryptadenia* they are subrotund, narrowly oblong, oblong or ellipsoid. In both genera the scales are either translucent-white or yellow. They are usually glabrous, except in *L. buxifolia* where they have long stiff trichomes at their apices. In all the *Lachnaea* species and in *C. laxa* the scales are basally attached to the hypanthium. In *C. filicaulis* the scales are basally and partly abaxially attached to the hypanthium, and in *C. grandiflora* and *C. uniflora* they are abaxially attached to the hypanthium.

Disc

A disc is absent in both genera.

Gynoecium

In *Lachnaea* the ovary is sessile, oblong, narrowly ellipsoid, ellipsoid, ovoid or obovoid, 0.5–4.4 × 0.2–2.5 mm, completely glabrous or glabrous with a tuft of hairs at the apex. In *L. filamentosa* the ovary is usually glabrous with a tuft of hairs at the apex but occasionally it may also be adpressed hairy and tufted at the apex.

In *Cryptadenia* the ovary is sessile, ellipsoid, 0.7–1.8 × 0.4–0.7 mm, usually glabrous, but in *C. filicaulis* it is
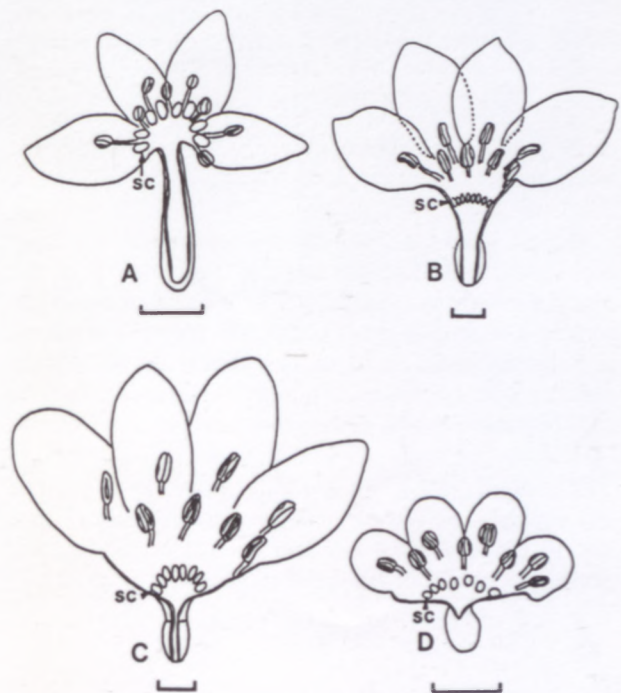

FIGURE 12.—*Cryptadenia*. Flowers split longitudinally with gynoecia removed. A, *C. laxa, I. Oliver 4*; B, *C. uniflora, Beyers 197*; C, *C. grandiflora, Beyers 151*; D, *C. filicaulis, Thompson 3789*. sc, scale. Scale bars: A–D, 2 mm.

Vascular anatomy of the flower

The basic vascular pattern is the same in both genera. The eight traces supplying the calyx, depart from the vascular tissue of the pedicel or the floral axis, where they are arranged in a continuous cylinder (Figure 14A) or in a ring of bundles (Figure 15A) in *Lachnaea* and in a continuous cylinder in *Cryptadenia* (Figure 16A). The eight sepal traces extend upwards in the hypanthium. The lateral bundles of the sepals arise commissurally after the departure of the antipetalous stamen traces (Figure 17A, C, G, H, I) or at the same point of departure of the antipetalous stamen traces (Figure 17B, D, E, F, J) at various levels on the hypanthium. The vascular supply of the sepals consists of a midrib bundle and two lateral bundles.

The stamens are single-trace organs. The antipetalous stamen traces are fused to the commissural sepal traces, and the antisepalous stamen traces to the sepal midrib traces at their point of origin from the stele. The stamen traces separate from the sepal traces in two whorls at different levels in the hypanthium. The antipetalous stamen traces diverge from the commissural sepal bundles before
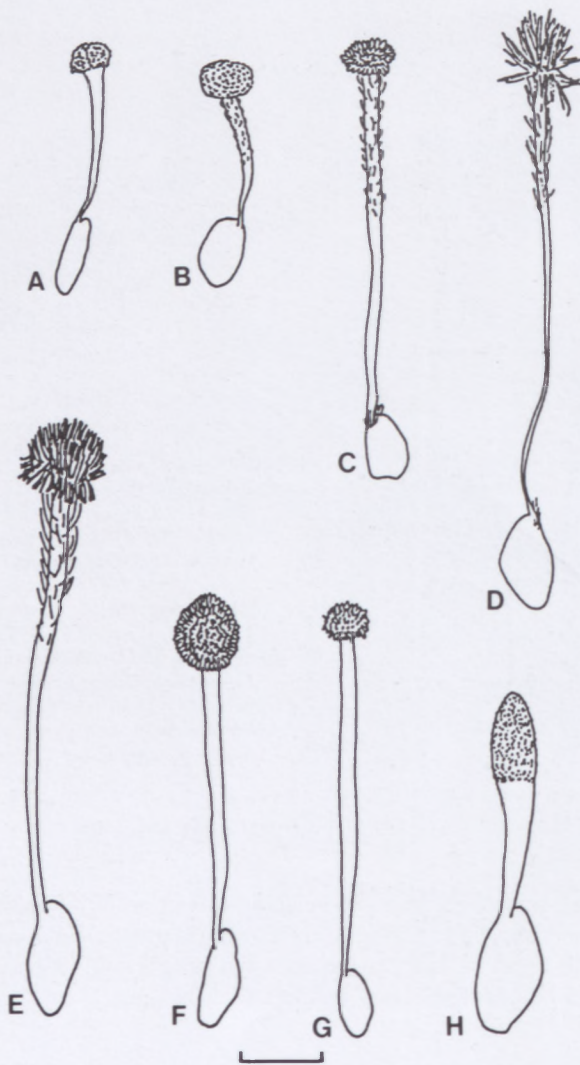

FIGURE 13.—*Lachnaea* and *Cryptadenia*. Gynoecia. A, *L. funicaulis, Marsh 758*; B, *L. ericoides, Beyers 172*; C, *L. ruscifolia, Goldblatt & Manning 8870*; D, *L. nervosa, De Kock 152*; E, *C. laxa, I. Oliver 4*; F, *C. uniflora, Beyers 197*; G, *C. grandiflora, Leighton BOL 21142*; H, *C. filicaulis, Thompson 3789*. Scale bars: A–E, H, 1 mm; F, G, 2 mm.

either glabrous or pubescent towards the apex on the side where the style is inserted.

In both genera the ovary is unilocular, with a solitary anatropous ovule laterally attached near the top of the ovary; the style is laterally attached, linear or linear-obconical. The style is either completely glabrous or pubescent in the distal third to two thirds, or completely pubescent in *Lachnaea*, whereas in *Cryptadenia* it is usually glabrous but in *C. laxa* the distal half is pubescent.

The stigma in *Lachnaea* is either brushlike or capitate and papillate, or capitate and elongate-papillate (Figure 13). In *Cryptadenia* it is either conical or capitate and elongate-papillate, or brushlike (Figure 13).

Fruit

The fruit in both genera is an achene which is enclosed in the persistent base of the hypanthium. The pericarp is dry and thin, whereas the seed coat is thick and crustaceous.
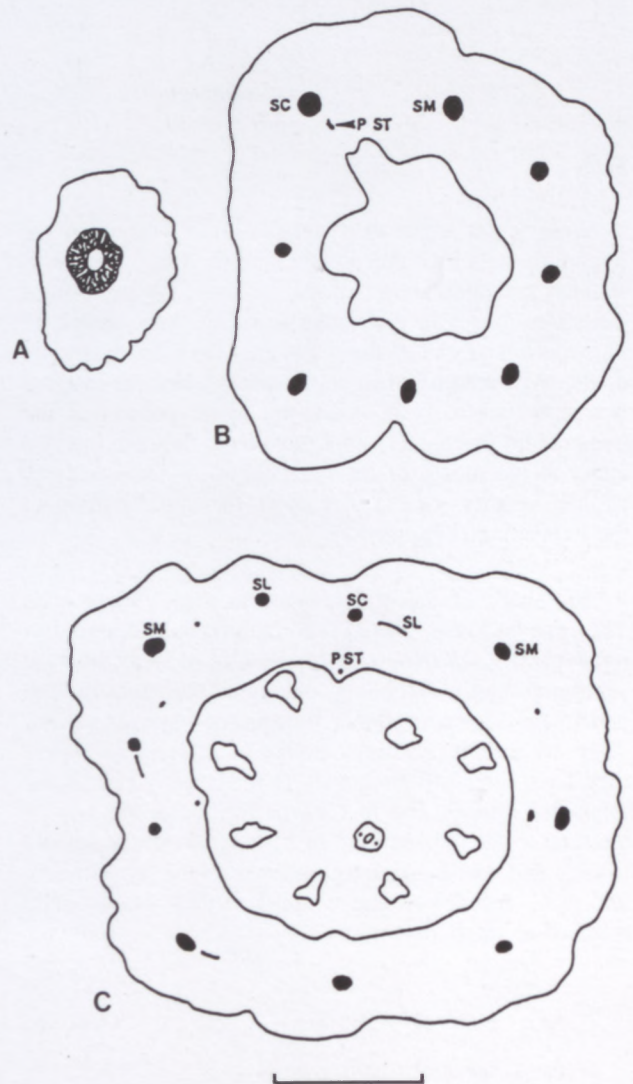

FIGURE 14.—*Lachnaea capitata, Beyers 128*. Floral anatomy. A, transection through floral axis. B, C, transections of flower: B, vasculature of hypanthium, separation of antipetalous stamen trace (P ST) from commissural sepal bundle (SC); C, splitting of commissural sepal bundles into sepal lateral bundles (SL). SM, sepal midrib bundle. Scale bar: 500 μm.
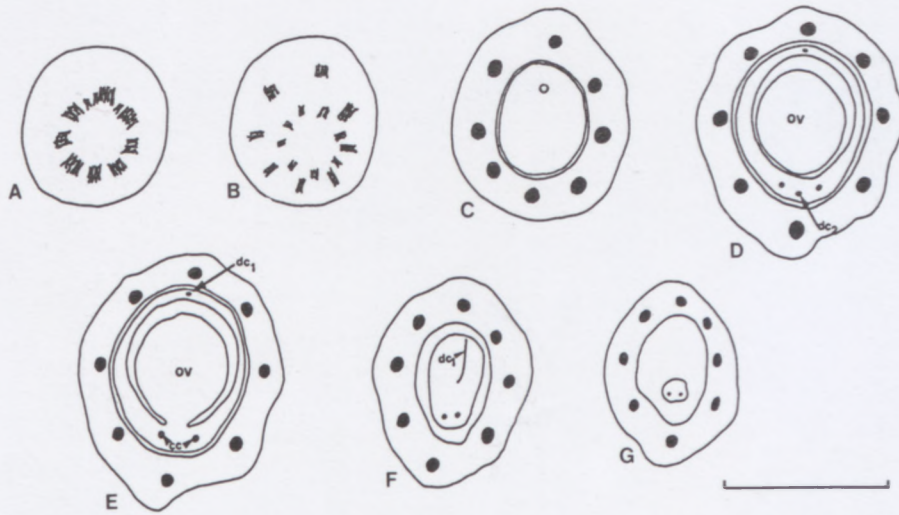
FIGURE 15.—*Lachnaea diosmoides*, *Beyers 151*. Transections of flower. A, pedicel showing ring of vascular bundles; B, base of hypanthium showing departure of whorl of eight bundles; C, hypanthium at base of ovary; D, lower portion of ovary; E, middle of ovary; F, top of ovary; G, base of style. o, ovary; ov, ovule; dc₁, dorsal carpellary of fertile carpel; cc, commissural carpellary; dc₂, dorsal carpellary of sterile carpel. Scale bar: 500 μm.

the antisepalous stamen traces diverge from the sepal midrib bundles (Figure 14). The antisepalous stamen traces leave the sepal midrib bundles at or just below the rim of the hypanthium, except in *C. filicaulis* (Figure 17H) where they depart a quarter of the way down the upper portion of the hypanthium. The antipetalous stamen traces leave the commissural sepal bundles at various levels on the upper portion of the hypanthium. In *L. buxifolia* (Figure 17F), *L. diosmoides* (Figure 17B), *L. eriocephala* (Figure 17D), *L. ruscifolia* (Figure 17E) and *C. laxa* (Figure 17J) these stamen traces depart near the rim of the tube, in *L. axillaris* (Figure 17C), *C. filicaulis* (Figure 17H), *C. grandiflora* (Figure 17I) and *C. uniflora* (Figure 17G) they depart midway and in *L. capitata* (Figure 17A) they depart three quarters of the way down the tube. The stamens become free from the hypanthium a short distance above the divergence of their traces as in *L. buxifolia* (Figure 17F) and *C. filicaulis* (Figure 17H), or are adnate to the hypanthium for some distance before becoming free as in *L. capitata* (Figure 17A) and *C. uniflora* (Figure 17G). In *L. buxifolia* (Figure 17F), *L. diosmoides* (Figure 17B), *L. eriocephala* (Figure 17D), *C. grandiflora* (Figure 17I) and *C. laxa* (Figure 17J) the antisepalous stamens are adnate to the basal portion of the sepals. In *Cryptadenia*, with the exception of *C. laxa*, the hypanthium, above the insertion of the scales, is further augmented by small median sepal bundles whose stelar extensions have been aborted (Figures 17G, H, I; 18A). Branches of these median sepal bundles may anastomose with the midrib bundles and the commissural sepal bundles. A rich vascular plexus exists in the hypanthium of *C. laxa* at the level of insertion of the scales (Figure 17J).

The eight scales arise as emergences from the adaxial wall of the hypanthium (Figure 19) at different levels on the upper portion of the hypanthium. They emerge a short distance below the divergence of the antipetalous stamen traces from the commissural sepal bundles, as in *L. capitata* (Figure 17A) and in *C. grandiflora* (Figure 17I), or just above the divergence of the antipetalous stamen traces and the lateral sepal traces from the commissural sepal bundles, as in *L. buxifolia* (Figure 17F) and in *C. laxa* (Figure 17J). No vascular tissue is present in or at the base of the scales, even in those taxa in which the scales are inserted in close juxtaposition to the sepal lateral bundles and the sepal midrib bundles. In *Lachnaea* the scales are usually non-glandular (Figure 20A) but in *L.*

axillaris (Figure 20B) they are composed of compact thin-walled cells rich in cytoplasm with large nuclei, thus appearing glandular (Esau 1965). Similarly in *Cryptadenia* the scales are either non-glandular or appear glandular. No secretion was observed from the scales in either genus.

The ovary is bicarpellate. In *Lachnaea* the dorsal carpellary bundle of the fertile carpel is always present, whereas the dorsal carpellary bundle of the sterile carpel is present in *L. capitata* and *L. diosmoides* (Figure 15), but absent in *L. eriocephala* (Figure 21) and *L. axillaris*. In *Cryptadenia* the dorsal carpellary bundle of the fertile carpel is usually present, but absent in *C. filicaulis* (Figure 16) whereas the dorsal carpellary bundle of the sterile carpel is always present (Figure 16).

FIGURE 16.—*Cryptadenia filicaulis*, *Oliver 9803*. A, transection through floral axis. B–D, transections of flower: B, base of flower showing departure of whorl of eight bundles; C, lower portion of ovary showing abortion of dorsal carpellary of fertile carpel; D, base of style showing commissural carpellaries and dorsal carpellary of sterile carpel entering style. cc, commissural carpellary; dc₂, dorsal carpellary of sterile carpel. Scale bar: 500 μm.

FIGURE 17.—*Lachnaea* and *Cryptadenia*. Vasculature of hypanthium, stamens and sepals. A, *L. capitata, Beyers 128*; B, *L. diosmoides, Beyers 151*; C, *L. axillaris, Beyers 197*; D, *L. eriocephala, Beyers 54*; E, *L. ruscifolia, Vlok 2084*; F, *L. buxifolia, Beyers 118*; G, *C. uniflora, Beyers 136*; H, *C. filicaulis, Oliver 9803*; I, *C. grandiflora, Beyers 196*; J, *C. laxa, I. Oliver 4*. Scale bar: 1 mm.

The commissural carpellary bundles (Heinig 1951) are closely associated with the dorsal bundle of the sterile carpel (Figures 15, 16), or when the latter is absent they are in the associated position (Figure 21).

The vasculature of the style is variable. It may consist of: the commissural carpellary bundles as in *L. diosmoides* (Figure 15), *L. axillaris* and *L. capitata*; the two ventral bundles of the sterile carpel arising from the split commissural carpellary bundles as in *L. eriocephala* (Figure 21); the dorsal bundle of the fertile carpel, the dorsal bundle of the sterile carpel and the commissural carpellary bundles as in *C. grandiflora*; the dorsal bundle of the sterile carpel and the commissural carpellary bundle as in *C. filicaulis* (Figure 16) and *C. uniflora*; or the dorsal bundle of the fertile carpel and the dorsal bundle of the sterile carpel as in *C. laxa*.

Pollen morphology

Pollen grains of the *Lachnaea* and *Cryptadenia* species examined, have the same basic morphology. The grains are monads, globose and polyforate (Figure 22) with a diameter of 22–52 μm in *Lachnaea* and 40–50 μm in *Cryptadenia* (Table 3).

The pollen is tectate and supra-ornate (Figure 22). Erdtman (1971) describes the sculpture pattern as crotonoid. The sexine is thicker than the nexine. The sexine is attached to the nexine by means of columellae, which unite into a tectum above. The tectum is reticulate with supratectal triangular projections. These supratectal structures are trihedral to shallowly trihedral with the basal sides straight as in *L. buxifolia* (Figure 23A), *L. ruscifolia* (Figure 23B) and *C. uniflora* (Figure 23E) or emarginate as in *L. aurea* (Figure 23C), *L. eriocephala* (Figure 23D) and *C. laxa* (Figure 23F). A vestigial spinule occurs at
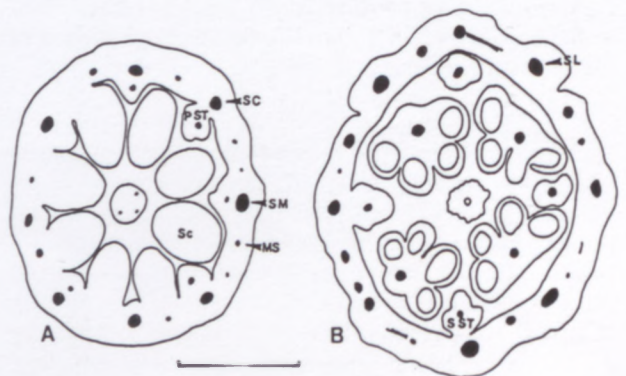

FIGURE 18.—*Cryptadenia filicaulis, Oliver 9803*. Transection of hypanthium of flower. A, at level where scales (Sc) separate from hypanthium; B, where antisepalous stamens (S ST) separate from tube. P ST, antipetalous stamens; SM, sepal midrib bundle; SC, commissural sepal bundle; SL, sepal lateral bundle; MS, median sepal bundle. Scale bar: 500 μm.

FIGURE 19.—*Lachnaea* and *Cryptadenia*. Floral anatomy of hypanthia. Vasculature and scales (Sc) arising from adaxial wall. A, *L. capitata*, *Beyers 128*; B, *C. grandiflora*, *Beyers 196*. SM, sepal midrib bundle; SC, commissural sepal bundle; Sc, scale; MS, median sepal bundle. Scale bars: A, B, 100 μm.

the base of each of the three main ridges in some *Lachnaea* species (Figure 23A, B) but was absent in all the *Cryptadenia* species (Table 4). The surface of the lateral sides of the supratectal trihedral projections is striate in all the species (Figure 23).

Karyology

The haploid chromosome number of n = 9 was observed in six species of *Lachnaea* and in two species of

Cryptadenia (Table 5). The meiotic chromosome behaviour was normal.

DISCUSSION

Habit, phyllotaxis and foliage

The habit, phyllotaxis and macromorphological characters of the foliage leaves are rather variable among the

FIGURE 20.—*Lachnaea*. Longitudinal section of scale. A, *L. capitata*, *Beyers 128*; B, *L. axillaris*, *Beyers 127*. Sc, scale. Scale bars: A, B, 50 μm.

TABLE 3.—Size range of pollen grains (mean followed by range in parentheses) in *Lachnaea* and *Cryptadenia*

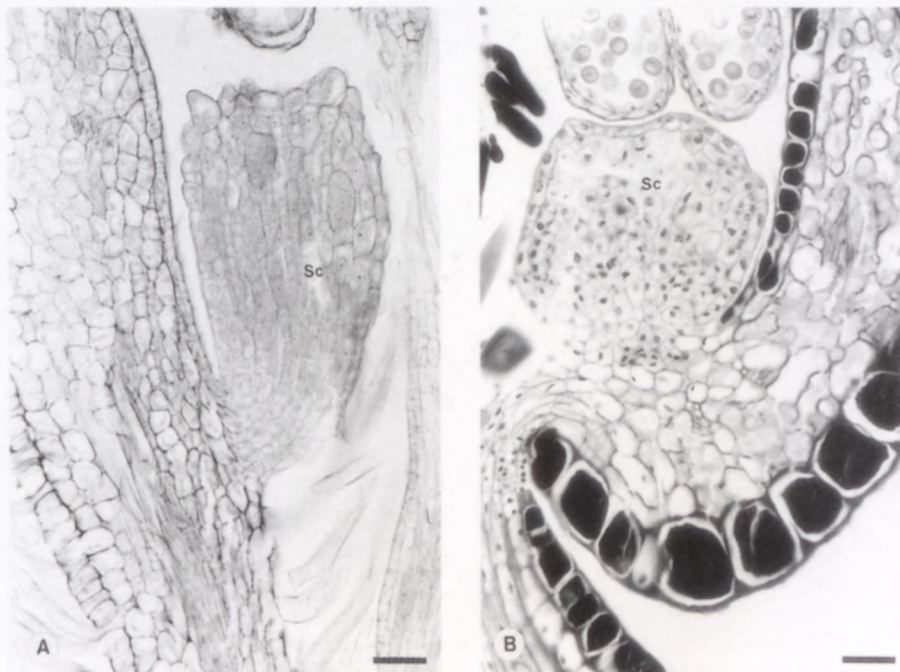| Taxon	Collector	Diameter (µm)
Lachnaea		
aurea	*Beyers 135*	47 (39–51)
axillaris	*Steyn 331*	22 (20–23)
burchellii	*Oliver 9241*	29 (23–37)
buxifolia	*Beyers 122*	47 (43–53)
	Beyers 118	52 (49–55)
	Taylor 8648	49 (47–59)
capitata	*Hugo 231*	26 (23–29)
	Beyers 128	29 (23–33)
densiflora	*Beyers 145*	29 (23–45)
	Beyers 117	32 (29–35)
	Beyers 115	27 (23–31)
diosmoides	*Beyers 181*	29 (23–33)
	Van Niekerk 53	30 (27–33)
ericoides	*McDonald 1842*	28 (25–31)
	Zeyher 3776	27 (23–31)
eriocephala	*Beyers 54*	50 (39–57)
	Spreeth 141	45 (39–55)
filamentosa	*Beyers 110*	45 (39–55)
	Taylor 10770	50 (47–56)
funicaulis	*Beyers 125*	25 (20–27)
nervosa	*De Kock 152*	35 (31–39)
penicillata	*Oliver & Fellingham 9145*	28 (19–35)
	Beyers 173	29 (23–39)
ruscifolia	*Vlok 2084*	35 (31–39)
Cryptadenia		
filicaulis	*Esterhuysen 34370*	33 (29–39)
grandiflora	*Beyers 151*	48 (45–58)
	Beyers 129	56 (47–64)
laxa	*Bolus 7875*	40 (33–43)
uniflora	*Haynes 477*	52 (49–55)
	Beyers 136	54 (47–62)

species and sometimes even within individual species of *Lachnaea* and *Cryptadenia*. The variation range within *Cryptadenia* is smaller than in *Lachnaea* but one must take into account that *Cryptadenia* is a much smaller group of species. With regard to the habit, phyllotaxis and

TABLE 4.—Comparison of sculpturing of supratectal projections of tectate pollen in *Lachnaea* and *Cryptadenia*

Taxon	Base sides		Vestigial spinules at base of main ridges
	± straight	emarginate	
Lachnaea			
aurea	–	+	–
axillaris	+	–	–
burchellii	+	–	+
buxifolia	+	–	+
capitata	+	–	+
densiflora	+	–	+
diosmoides	+	–	+
ericoides	–	+	–
eriocephala	–	+	–
filamentosa	–	+	+
funicaulis	–	+	–
nervosa	+	–	+
penicillata	+	–	+
ruscifolia	+	–	+
Cryptadenia			
filicaulis	+	–	–
grandiflora	+	–	–
laxa	–	+	–
uniflora	+	–	–

TABLE 5.—Chromosome numbers of *Lachnaea* and *Cryptadenia* species studied

Taxon	Haploid chromosome number	Voucher specimen
Lachnaea		
buxifolia	9	*Beyers 122*
densiflora	9	*Beyers 145*
diosmoides	9	*Beyers 181*
ericoides	9	*Beyers 172*
eriocephala	9	*Beyers 54*
funicaulis	9	*Du Toit s.n.*
Cryptadenia		
filicaulis	9	*McDonald 1989*
uniflora	9	*Beyers 136*

macromorphological characters of the foliage leaves no major differences were found which could be used to demarcate the two genera.

Based on the anatomy of the leaves, two leaf groups can be distinguished within *Lachnaea*: 1, those which are amphistomatic and either isobilateral or almost centric; 2, those which are epistomatic and either isobilateral or dorsiventral. The leaves of *Cryptadenia* are epistomatic and either almost isobilateral or dorsiventral. The anatomy of the latter resembles that of the second group in *Lachnaea*. Similar cuticular patterns, namely unsculptured, minutely papillate or undulate, occur in both genera. These characters confirm the close relationship between *Cryptadenia* and *Lachnaea*.
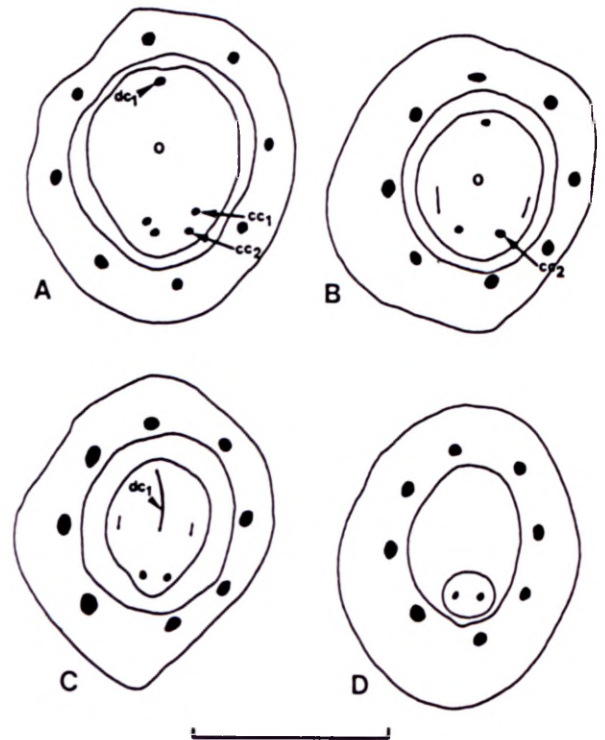

FIGURE 21.—*Lachnaea eriocephala, Beyers 54.* Transections of flower: A, base of ovary; B, upper portion of ovary; C, top of ovary; D, base of style. o, ovary; dc_1, dorsal carpellary of fertile carpel; cc_1, commissural carpellary of fertile carpel; cc_2, commissural carpellary of sterile carpel. Scale bar: 500 µm.
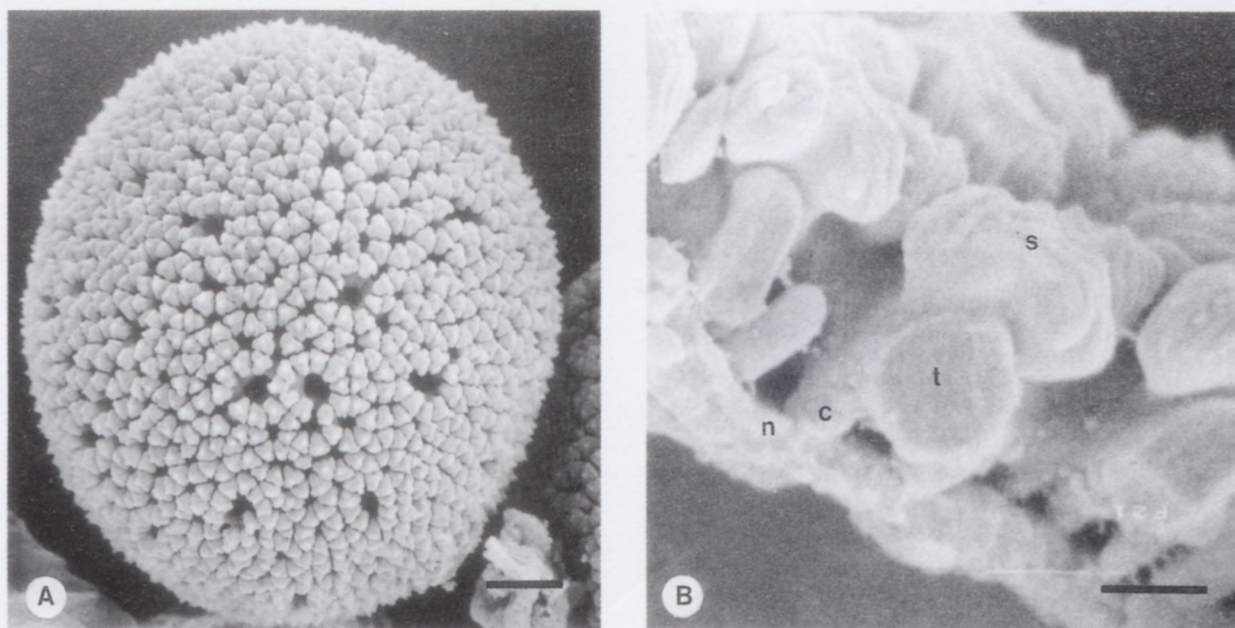
FIGURE 22.—*Lachnaea* and *Cryptadenia*. SEM micrographs of pollen morphology. A, *L. aurea, Beyers 135*, pollen grain; B, *L. buxifolia, Beyers 122*, transection of pollen grain wall. n, nexine; c, columella; t, tectum; s, supratectal structure. Scale bars: A, 5 μm; B, 1 μm.

Morphology of flower and fruit

Pedicel/floral articulation

The study of the floral morphology revealed the strong similarity between *Lachnaea* and *Cryptadenia*. Sessile flowers are found in both genera. The ring of trichomes at the base of the flower, occurring at the floral articulation, corresponds to that found by Heads (1990) in *Kelleria* Endl. This structure, according to Heads (1990) is reminiscent of the calycular pappus of many members of the Asteraceae and the peltate hairs of Elaeagnaceae, and could be regarded either as a compressed pubescent 'pedicel' or as the 'calyx' of a sessile flower. The pedicels of pedicellate flowers of *Lachnaea* species are always pubescent. The trichomes at the floral articulation do not differ from those on the pedicel and it is therefore more acceptable to regard the ring of trichomes at the base of the sessile flowers as a compressed pubescent 'pedicel'.

Hypanthium

The nature of the hypanthium of the flower of the Thymelaeaceae has been interpreted as being appendicular (foliar) and representing a calyx tube by Meisner (1857), Wright (1915), Peterson (1959) and Dyer (1975), or as being receptacular by Eichler (1878), Baillon (1880), Gilg (1894), Wettstein (1935), Rendle (1938) and Bunninger (1972). According to Lawrence (1951) the hypanthium is more commonly and inaccurately termed the calyx tube or floral tube. Heads (1990), Heinig (1951) and Saunders (1939) regard the floral tube of the Thymelaeaceae as a hypanthium. The vascular anatomy undertaken in this study has shown that the floral tube in both genera can be regarded as a hypanthium.

The position of the plane of circumscision expressed as a percentage of the total length of the hypanthium varies in both genera between 20% and 80%. The shape,

length and pubescence of the hypanthium of *Cryptadenia* falls well within the variation range found in *Lachnaea*.

Calyx

The sepals in *Lachnaea* vary from being almost equal to distinctly unequal. The transition from one form to the other is gradual. The sepals of *Cryptadenia* are almost equal which was one of the reasons why Baillon (1880) incorporated *Cryptadenia* as a section in *Lachnaea*.

The aestivation of the sepals is the same in both genera and a basic floral vascular pattern is common to both genera.

Androecium

Eight stamens in two whorls of four each are present in both genera. The position of insertion on the floral tube shows a varying degree of adnation within both *Lachnaea* and *Cryptadenia*. The stamens are always exserted in *Lachnaea*, but in *Cryptadenia* they are either exserted or only the antisepalous stamens are fully exserted.

Scales

In the different genera of the Thymelaeaceae organs comparable to the scales in *Lachnaea* and *Cryptadenia* have been interpreted by various authors as petaloid glands, scales, mere outgrowths of the perigynium, aborted stamens, squamellae which should be regarded either as new structures of uncertain origin or as modified parts of the androecium, stipules or petals which might be reduced or greatly modified in form (Heinig 1951).

In *Lachnaea* various views regarding the nature of these scales have been expressed, namely that they should be regarded as staminodes, scales, glandular or scale-like receptacular effigurations, or petaloid scales homologous
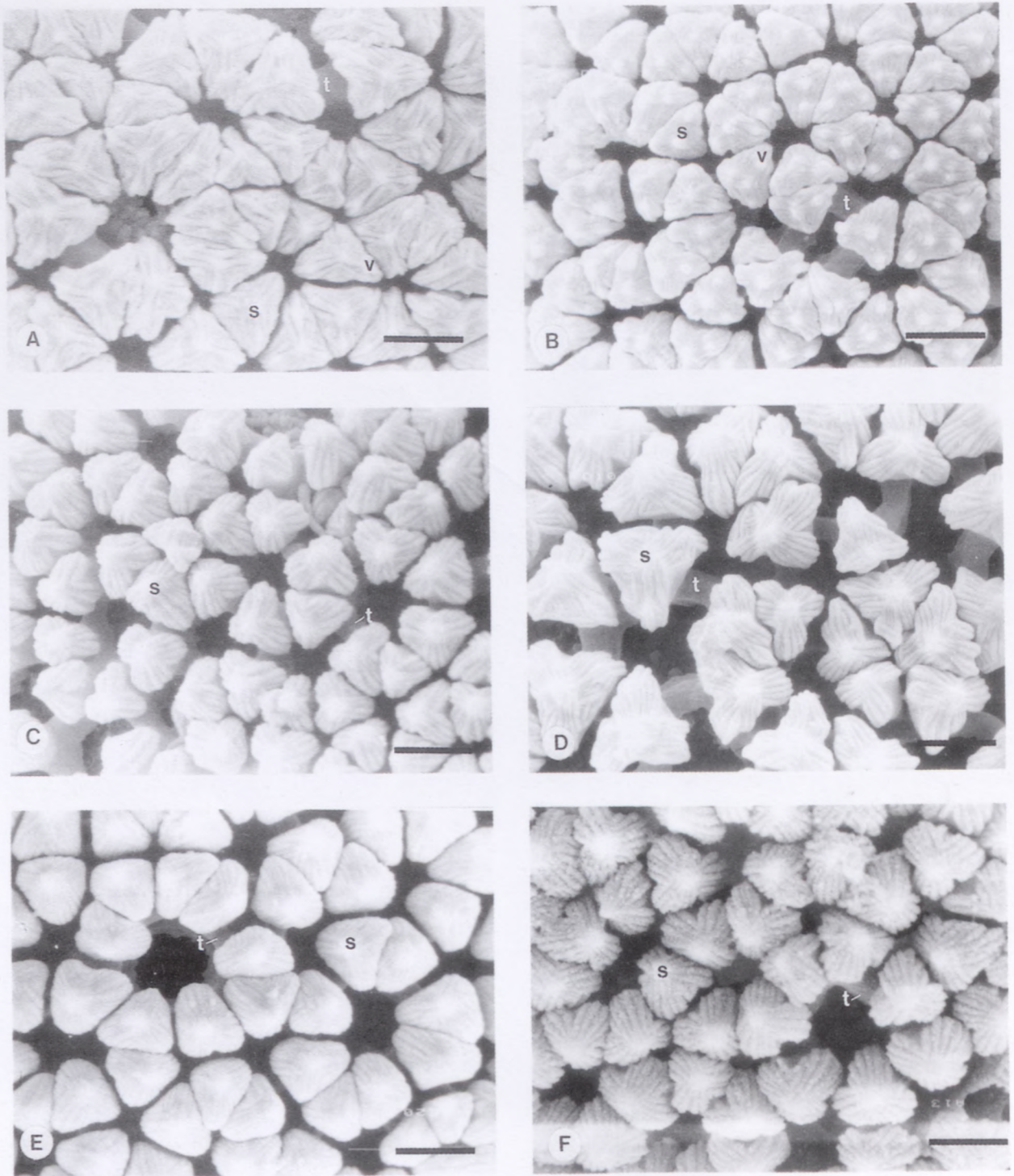
FIGURE 23.—*Lachnaea* and *Cryptadenia*. SEM micrographs of pollen grains. A, *L. buxifolia*, *Beyers 122*; B, *L. ruscifolia*, *Vlok 2084*; C, *L. aurea*, *Beyers 135*; D, *L. eriocephala*, *Beyers 54*; E, *C. uniflora*, *Haynes 477*; F, *C. laxa*, *Bolus 7875*. s, supratectal structure; t, tectum; v, vestigial spinule. Scale bars: A–F, 2 μm.

to petals. In those species of *Lachnaea* where these structures are narrowly straplike or filiform, Domke (1934) regarded them to be in their original form and for that reason Meisner (1840), according to Domke (1934), mistakenly considered them to be staminodes. These structures, in their original position according to Domke (1934), are inserted at the base of the calyx lobes and slightly higher than the insertion of the antipetalous stamens but through zygomorphy these structures have positioned themselves in a single whorl at the same height as, or sometimes below, the filament insertion. This situa-

tion is not met in other genera such as *Gnidia* and *Struthiola*, where the petal-like structures are inserted above the insertion of the filaments at the mouth of the tube. From the vascular anatomy of the flowers one would rather believe the converse, namely that the scales were originally positioned below the antipetalous stamen whorl and through zygomorphy have been slightly displaced to above the antisepalous stamen insertion, as in *L. filamentosa*. Heinig (1951) considered these structures to be stipules of the calyx lobes and found no reason to consider them to be vertical extensions of the disc as Gilg (1894)

did. Taxonomists have not been eager to accept the interpretation of the petaloid scales as stipules on the grounds that stipulate sepals would not occur in a group in which the foliage leaves are exstipulate. Heinig (1951) supported her interpretation on the grounds that the absence of stipules on the foliage leaves and the presence of stipular appendages in the floral organs should be considered another aspect of the progressive reduction from a more primitive state. Heads (1990) rejects Heinig's interpretation of the petaloid scales being stipules on the grounds that she used the concepts of 'leaf' and 'stipule' of Eames & MacDaniels (1948) which were in turn derived from Van Tieghem's (1871 in Heads 1990) morphology which he regards as being fundamentally flawed. Heads (1990) refers to the comparable organs in *Kelleria* as gland scales.

In *Cryptadenia*, as in *Lachnaea*, different views regarding the scales have been expressed. They have been referred to as glands, scales, glandular or scale-like receptacular effigurations, or petaloid scales. Although Domke (1934) referred to them as 'glands', he regarded them as petaloid scales homologous to those of *Lachnaea*. According to Domke (1934) the 'effigurations' in *L. axillaris*, *L. diosmoides* and *L. ericoides*, because of their position and shape, lead directly to those in *Cryptadenia* where these structures are nearly completely attached abaxially to the hypanthium.

Because of their position and anatomy, we regard these structures in both *Lachnaea* and *Cryptadenia*, as scales which are mere emergences of the adaxial wall of the hypanthium.

The position of the scales in both genera is usually below the insertion of the antipetalous stamens. In the more zygomorphic forms in *Lachnaea* and in one species of *Cryptadenia*, where they are in close juxtaposition to the stamens, they emerge between the insertion of the antipetalous and antisepalous stamens. The position of the scales in the upper portion of the hypanthium is variable in both genera. Those of *Lachnaea* are inserted at the mouth of the hypanthium to midway down the upper portion of the hypanthium, whereas those in *Cryptadenia* are inserted at the mouth of the hypanthium to three quarters of the way down the upper portion of the hypanthium. On the grounds of the position of the scales, a generic character used by Meisner (1840, 1857), no cutoff point can be made to separate the two genera as the displacement of the scales is gradual. In both genera the scales may be non-glandular or glandular. Another generic character which Domke (1934) used, was the attachment of the scales to the hypanthium. According to him the scales in *Lachnaea* are basally attached, whereas those in *Cryptadenia* are abaxially attached. In *L. axillaris* the cup-shaped and sigmoid basal part of the upper portion of the hypanthium gives the impression that the scales are basally attached. If however, the sigmoid curve is removed by extending the hypanthium upwards, the scales would in fact be abaxially attached and would correspond to the situation in the flower of *C. filicaulis*.

Gynoecium

The ovary in both genera is sessile, pseudomono-merous (consisting of one expanded or fertile carpel and one contracted or sterile carpel) and unilocular with a solitary anatropous ovule laterally attached near the top of the ovary. The style is always laterally attached to the ovary. The stigma is either brush-like or capitate in both genera but may also be conical in *Cryptadenia*.

Zygomorphy is expressed in both genera through the lateral placement of the style and the single locule.

Fruit

In both genera the fruit is an achene which is enclosed within the persistent base of the hypanthium. According to Domke (1934) the achene is, without exception, characteristic of the Thymelaeoideae and thus at the generic level the fruit is not of taxonomic importance.

Pollen morphology

The pollen grains of *Lachnaea* and *Cryptadenia* have the same basic morphology. Based on the sculpture of the supratectal structures two pollen grain types can be distinguished within *Lachnaea*, namely those with vestigial spinules at the base of the three main ridges and those without spinules. In *Cryptadenia* the supratectal structures are devoid of spinules at the base of the three main ridges and are thus similar to the latter pollen grain type of *Lachnaea*. Furthermore, in both genera, the lateral sides of the trihedral structures are striate and the basal sides are either straight or emarginate. The pollen grain size, following Radford *et al.* (1974), is medium to large in *Cryptadenia* and small to large in *Lachnaea*. This feature, therefore, also overlaps in the two genera.

Karyology

In most Thymelaeaceae the haploid chromosome number (n = 9) and the somatic chromosome number (2n = 18) have been observed (Nevling & Woodbury 1966 in Orloduff 1968. The following references are given in Moore 1973: Sharma & Sarkar 1967, 1968, Bjorkquist *et al.* 1969, Delay 1969, Gupta & Gillett 1969, Majovsky *et al.* 1970. Bhat *et al.* in Löve 1974. In Moore 1977: Kuzmanov 1973, Loeve & Kjellqvist 1974, Majovsky *et al.* 1974. Heads 1990). Polyploidy has been recorded in *Daphne* (Heads 1990), *Daphnopsis* (Nevling & Woodbury 1966 in Orloduff 1968), *Edgeworthia* Meisn. (Heads 1990), *Pimelea* Banks & Sol. (Heads 1990), and *Wikstroemia* Endl. (Gupta & Gillett 1969 in Moore 1973; Heads 1990).

The chromosome number of *Lasiosiphon eriocephalus* Decne., according to Subramanyan & Kamble in Löve 1967, is n = 8. The genus *Lasiosiphon* Fresen. was incorporated in the genus *Gnidia* for southern Africa (Dyer 1975). Although the above species is not indigenous to South Africa, it was the only chromosome number previously available for a genus of the Thymelaeaceae represented in South Africa.

The chromosome counts of n = 9 here reported for the species of both *Lachnaea* and *Cryptadenia*, are the first records for these two genera. The basic chromosome number of × = 9 was recorded for most genera of the

TABLE 6.—Comparison of characters in *Lachnaea* and *Cryptadenia*

Character	*Lachnaea*	*Cryptadenia*
Habit	shrubs or shrublets multi- or single-stemmed at base, 0.15–2.0 m tall	shrublets multi- or single-stemmed at base, 0.12–0.8 m tall
Phyllotaxis	alternate or decussate	decussate
Flower	hermaphrodite, tetramerous	hermaphrodite, tetramerous
Hypanthium	circumscissile	circumscissile
Position of circumscision zone above base of hypanthium	$\frac{1}{5}$–$\frac{4}{5}$	$\frac{1}{5}$–$\frac{4}{5}$
Basal portion of hypanthium	ellipsoid, widely ellipsoid, ovoid, widely ovoid or obovoid	ovoid or ellipsoid
Upper portion of hypanthium	funnel-shaped, cylindrical, obconical, cup-shaped or cup-shaped with a sigmoid curve	funnel-shaped or cup-shaped
Stamens	4 + 4, exserted	4 + 4, exserted or semi-exserted
Stamen insertion	epipetalous to third of the way down upper portion of hypanthium	epipetalous to three quarters of the way down upper portion of hypanthium
Floral scales	8, non-glandular or glandular	8, non-glandular or glandular
Scale insertion	mouth of hypanthium to midway down upper portion of hypanthium	mouth of hypanthium to three quarters of the way down upper portion of hypanthium
Style	lateral	lateral
Stigma	brush-like or capitate	brush-like, capitate or conical
Fruit	dry, enclosed in persistent base of hypanthium	dry, enclosed in persistent base of hypanthium
Leaf anatomy	epistomatic, isobilateral or dorsiventral; or amphistomatic, isobilateral or almost centric	epistomatic, almost isobilateral or dorsiventral
Pollen grains	monads, globose, polyforate, 22–52 µm in diameter, tectate and supraornate	monads, globose, polyforate, 40–50 µm in diameter, tectate and supraornate
Sculpture of supratectal structures	vestigial spinules present or absent, lateral sides of trihedral structures striate	vestigial spinules absent, lateral sides of trihedral structures striate
Chromosome number	n = 9	n = 9

Thymelaeaceae and can therefore not be used to demarcate genera.

CONCLUSIONS

The Thymelaeaceae is a family in which it is difficult to find sound characters for generic delimitation. According to Peterson (1959), only a few characters can be used and they are of superficial significance. While revising the thymelaeaceous genera of the African continent, Peterson (1959) experienced difficulties with the classification. According to him these difficulties were not so much connected to the species concept but rather to the delimitation of genera which showed morphologically continuous characters which merged them into each other.

According to Baillon (1880), the only other worker who has discussed generic characters in the Thymelaeaceae, the following characters are generally of generic value:

* the number of floral parts,

* the point of insertion of the stamens and the dimension of their filaments which render them exserted or enclosed,

* presence or absence of the scales in the throat of the hypanthium,

* presence or absence of a disc at the base of the gynoecium,

* whether the base of the hypanthium is shed or persists growing around the ripe fruit, and

* the arrangement of the inflorescence.

In evaluating the results obtained from the present multidisciplinary study, consideration was given to those characters which Baillon (1880) advocated as being of value at generic level as well as those used by Heads (1990) to illustrate the major differences between *Kelleria* Endl. and *Drapetes* Lam. The results of this multidisciplinary approach, as summarized in Table 6, illustrate the great similarity between *Lachnaea* and *Cryptadenia*. These also show that several characters within *Lachnaea* exhibit a variation range which includes the variation in *Cryptadenia*, and that in a few other characters the variation range is extended in *Cryptadenia*. No distinguishing characters of generic value were found to support the present demarcation of *Lachnaea* and *Cryptadenia*. Furthermore Beyers & Van der Walt (1994) concluded that the inflorescence morphology revealed no distinct differences between *Lachnaea* and *Cryptadenia*.

With the view of establishing natural genera, and on the basis of the findings of this multidisciplinary study, we support the viewpoint of Baillon (1880) that *Cryptadenia* should be included within *Lachnaea*. A detailed taxonomic treatment of *Lachnaea sensu lato* should now be undertaken.

ACKNOWLEDGEMENTS

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